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The shape and the strength of the long bones of higher primates are related to two factors, the body size of the primate and its particular locomotor pattern. The analysis of bone strength, bone proportions and body proportions in higher primates depends on the separation of the effects of these two factors. Allometry (the scaling of characteristics against body size) is applied as an analytical technique for this purpose. Interspecific allometric analyses are carried out on 21 metrical variables representing body size, long bone length, limb length, the size of the cross section of the long bones and the strength of the cross section of the long bones. These analyses are based on a sample of 272 extant higher primates representing 32 species and on 17 fossil higher primates representing 13 species.

With attention to the basic assumptions involved in the interpretation of allometric relationships, the results of these analyses are discussed in the context of the mechanical requirements of the diverse locomotor patterns found among the extant higher primates. This information is also discussed in relation to the interpretation of the locomotor patterns of fossil higher primates as well as in relation to the course of higher primate locomotor evolution. Among the main conclusions that emerge from these analyses is the extreme specialization of the bone and limb proportions of the extant great apes, and not of Homo sapiens, in relation to the allometric trends in the smaller bodied higher primates. The New World primate, Alouatta, as well as some of the Miocene hominoids, are most similar in their bone and limb proportions to extant Homo sapiens when allometric relationships are taken into consideration. In addition, these primates represent a likely ancestral condition from which not only Homo sapiens, but also the specialized extant great apes could have evolved. Both the extant as well as the fossil Old World monkeys are markedly different in the allometry of their limb proportions from the New World monkeys, the majority of the Miocene hominoids as well as from the extant hominoids. The general locomotor pattern of the Old World monkeys which is associated with the above branch feeding adaptation as well as with the specialized features of their bone and limb proportions, is excluded as a plausible ancestral locomotor stage through which the extant hominoids would have passed.

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I. Introduction

I. Introduction

The significance of the analysis of the shape and strength of the primate post cranial skeleton lies in two related areas. Firstly, it lies in the determination of the morphological correlates of the diverse forms of locomotion characterising extant primates. The skeleton is a complex lever and support system that has the dual function of propelling and supporting the body. As a result, both the locomotor capability as well as the body weight of a animal are recorded in its skeleton. Secondly, the significance of morphological analysis lies in the interpretation of the locomotor capabilities of the fossil primates. Once the relationship between locomotor capability, body size and skeletal morphology is determined for living primates, this information can be used in comparison to infer the locomotor pattern and body size of fossil primates from their skeletal morphology. This information, combined with the analysis of the diet and the environment of the fossil primates, results in an understanding of the fossils as living animals as well as in a picture of the sequential development of primate locomotor patterns throughout the fossil record.

In the past, the gross size and shape of the primate skeleton has been analysed through the use of indices. Indices have taken the form of the length of a bone, or the size of the cross section of a bone, divided by another variable such as another bone length, body size or the length of the trunk. The Intermembral Index, the Robusticity Index, the Brachial Index and the Crural Index are all examples of this type of an approach. Although indices have resulted in the establishment of general differences in the primate skeleton between either taxonomic groups or locomotor groups, the specific significance of these indices is difficult to interpret. A change in size or in shape of a bone may result from either a change in the body size of a primate or from a particular locomotor specialisation independent of body size. Indices do not separate the effects of these two factors. If the two variables comprising the index do not change in size at the same rate, or isometrically, in primates of different body sizes, radically

different indices result, even though there may be an essential similarity when body size is taken into account. This problem is accentuated if one of the variables comprising the index is body weight. Body weight is proportional to body volume and would increase in proportion to a linear measurement cubed. Therefore, even if geometrical similarity (identity of proportions) exists in primates of different sizes, indices involving body size would obscure this homogenity.

Allometry (the scaling of characteristics against body size) is a superior technique for the analysis of the skeleton in primates of different body sizes. It employs logarithmic transformations to correct for differential increase between variables and uses bivariate plots to illustrate constant proportional relationships. It therefore clearly separates those features that change in size, or in shape, as a consequence of change in body size from those features that change as a consequence of change in locomotor adaptation.

Although allometry has been used in the analysis of morphological characteristics since the late 19th century, it has not been applied comprehensively to the analysis of the primate post cranial skeleton. In the following study, interspecific allometric analyses are carried out on 21 metrical variables representing body size, long bone length, limb length, the size and the shape of the cross section of the long bones and the strength of the cross section of the long bones. These analyses are based on a sample of 272 extant higher primates representing 32 species and on 17 fossil primates representing 13 species.

The interpretation of the results of allometric analyses are dependent on the assumptions made during the analysis and on the assumptions surrounding the particular statistical techniques employed. These assumptions include the nature of the sample employed, the validity of the statistical techniques used to characterise the relationships, the significance attributed to the variation around the allometric trend, and the validity of the relationship between the actual metrical parameters used in the analysis and the specific dependent or independent variables they

are assumed to represent.

With attention to these basic assumptions the results of the allometric analyses of the higher primate post cranial skeleton are discussed in the context of the mechanical requirements of the diverse locomotor patterns found among the extant higher primates as well as in relation to the interpretation of the locomotor patterns of fossil higher primates and to the course of higher primate locomotor evolution. In all of these areas allometry provides new insights into the significance of data that, in may cases, has been long available.

II. The Shape and Strength of Long Bones in the Higher Primates -- a Literature Review

11. 1. Introduction

The literature concerning the interpretation of the shape and strength of long bones in the higher primates has revolved around the concept of robusticity. The concept has been used in two separate contexts.

The first refers to the relationship between body size and cross-sectional diameter or circumference of the bone. The second refers to the relationship between the length of a bone and the diameter or circumference of its cross-section. In the first, the cross-section of the limb bones of a large animal would be expected to be relatively larger or more robust than the cross-section of the limb bones of a smaller animal. If an animal is equated to a cube supported by a short column, the weight of the animal would be proportional to the volume of the cube (or to one of its sides cubed), and the strength of the supporting column in compression would be proportional to the area of its cross-section (or to its diameter squared). Therefore, the weight of the cube would increase at a more rapid rate than the ability of the column to support that weight. Holding other factors constant, this tendency could be avoided if the area of the cross-section of the column increased at a rate proportional to the increase of the weight of the cube. In order to achieve this, the diameter of the cross-section must increase according to the $^{3}/2$ power of the cube root of body weight. In animals, however, this relationship is rarely observed. There are variables in addition to weight that affect the magnitude of the load a limb must support and variables other than size of the cross-section which affect the ability of the limb to support the load. These additional variables complicate the interpretation of robusticity in this context.

Robusticity used in the second context, the relationship between limb length and the size of its cross-section, is even more difficult to interpret than the first. Limb length is not a simple reflection of one causative factor. It can vary with

both body size and the locomotor pattern of the animal. To interpret robusticity in this second context it is necessary to distinguish the effects of these two factors on limb length as well as to clarify the relationship between the size of the cross section and the ability of the limb to support the load to which it is subjected.

In Anthropology and Primatology robusticity has most frequently been used in the second, more complicated, context. Therefore, as a background to the subsequent discussion of the functional, taxonomic and evolutionary significance of the shape and strength of limb bones in the high primate, literature in the following areas will be reviewed ·

1. The Concept of Robusticity
2. The Relationship between Limb Length, Bone Length and Locomotor Pattern in the higher Primates
3. Limb Length, Bone Length and the Morphology of the Last Common Ancestor of Man and the Apes
4. Limb Length and Bone Length in the Plio-Pleistocene Hominids
5. The Allometry of Primate Limb Length and Bone Length

11. 2. The Concept of Robusticity

The literature on the concept of robusticity will be divided into three sections. The first will review the early work on the concept of robusticity. The second will cover the literature on the mechanical significance of the cross-section of the long bones. The third will review the literature on the relationship between bone robusticity and body size.

11. 2. A. Early Literature Concerning Bone Robusticity

This section will summarize the literature on robusticity from the first mention of this subject in 1638 by Galileo Galilei to the middle of the 1930's. Until the 1920's the literature was entirely theoretical in nature. Various loading models were used to predict the limb proportions necessary to ensure that the limbs

of larger animals were as strong as the limbs of smaller animals relative to body weight. Only in the 1920's and 1930's were some of these theoretical predictions tested on empirical data. By the middle of the 1930's, however, it had become apparent that the question of strict physiological similarity in relation to body weight and bone strength was invalid. Work during the late 19th and early 20th centuries on the mechanics of human bone had shown that bones are adapted to the specific forces which they experience using a minimum of material. The focus of subsequent analyses was the description and/or explanation of the robusticity and loading relationships oberved in empirical data.

Galilei, in 1638, was the first to discuss the relationship between the size of an animal and its locomotor function. He noted that as an animal increases in size its weight necessarily increases much more rapidly than the ability of the limbs to support that weight. He reasoned that the strength of a limb was proportional to the area of its cross-section, an idea grounded in principles of basic engineering, which show that when a column is loaded in compression the load is distributed evenly over the area of the cross-section. Therefore, the maximum stress in the column, given a certain load, is proportional to that load divided by the area of the cross-section. He also assumed that the load carried by the supporting limbs was proportional to the volume of the animal, by definition, a cubed measurement. Therefore, as the animal increased in size, the load (a cubed measurement) would increase more rapidly than the ability of the limb to support that load (a squared measurement).

Galilei recognised two ways to maintain the necessary strength of the limbs relative to body weight. Firstly,

the area of the cross-section could be disproportionately increased to maintain the same stress per unit area as the animal increased in size. Secondly, the limb could be constructed from a stronger material which would withstand the increased stress as the weight of the body increased. In more modern terminology, either of these solutions would maintain 'physiological similarity' in the bones of larger animals. Galilei correctly recognised that only aquatic animals could escape the necessity of incorporating one of these alternatives. Weight support is not a critical factor in an aquatic environment, and larger animals could maintain the same limb proportions as smaller animals or increase in size according to 'geometrical similarity.'

The second mention of the relationship between size and function was in 1710 in Borellius' 'De motu animalium'. Borellius was primarily interested in the relationship between body size and locomotion, particularly jumping and leaping, but made a passing reference to Galilei's argument that larger animals must have more robust bones than smaller animals. Borellius overlooked Galilei's second alternative for maintaining physiological similarity, however, which was that the bones may be made from a stronger substance, and, as a result, his assertion that larger animals must have more robust bones than smaller animals is not entirely correct.

There is little direct reference to limb robusticity until the middle of the 19th century. Herbert Spencer (1847) expanded significantly on Galilei's argument that the strength of a limb loaded in compression was proportional to its cross section. He pointed out that this is also the case when the limb is loaded in tension, bending or torsion. Not only did Spencer generalise Galilei's argument, but he also observed the relatively reduced agility that characterises larger animals, a concept rooted in Borellius'

analysis (1710) which showed that the pull of the muscles is proportional to their cross-sectional area. Body weight or volume would, therefore, increase at a much faster rate than would the strength of the muscles and, relative to body size, the muscles of larger animals would be weaker than those of smaller animals. Although Spencer did not recognise the significance of this reduced relative muscle strength to the load born by the bones, it was to be a major topic of discussion in the 20th century.

Throughout the last half of the 19th century there was only passing reference to the mechanical determinants of skeletal robusticity. In particular, Wall (1851) discussed the large size of whales which are not limited by the mechanical requirements of terrestrial animals. Walton (1868) discussed the 'debility' of larger animals and trees from both the static and dynamic perpective, and Rauber (1882) rediscovered Galilei's 1638 discussion of physiological similarity. He published a short article bringing it to the attention of contemporary scientists working on skeletal mechanics.

The late 19th century, however, was characterised by growing interest in the mechanical adaptation of human bone. Based on the pioneer work of Ward (1838), Wyman (1857), Engel (1851) and Humphry (1858) the idea that the distribution of bone followed specific rules gained acceptance. In 1867 von Meyer, with the help of Culmann, investigated trabecular trajectories calculated on the model of a crane. Wolff (1892, 1899) extended the mechanical explanation of bone distribution to the orientation of trabeculae in deformed bone.

The shape of the cross-section and the distribution of cortical bone within the cross-section was first discussed by Rauber (1876, 1877) in the context of his hypothesis that a bone is a structure of equal strength. According to this hypothesis, bone is adapted to the forces

to which it is subjected in normal life and only to those forces. Therefore, every point on a bone is as strong as any other point on that bone relative to the force to which it is normally subjected. Roux (1885, 1895) expanded on this idea and on the basis of his analysis of an ankylosed knee joint formulated the Maximum-Minimum Law. This law states that in its outer form and fine structure, a bone is functionally constructed to combine maximum strength with minimum material.

At this time increased attention was paid to the critical forces to which a bone must adapt. Failure due to buckling was added to failure in tension, bending and torsion. Failure in buckling occurs when a column is slender. Under an axial load it will bend at the middle and fail as a result of this bending before it fails in compression. Rauber (1877), Messerer (1880) and Ghillini (1899) strongly favoured buckling as the factor which determined bone form while other contemporary anatomists supported strongly failure in bending or torsion.

D'Arcy Thompson, in his comprehensive work, Growth and Form (1917) summarised the effects of bending, buckling and compression on skeletal proportions in animals of different sizes. In addition, he related muscle strength and metabolism to body size and discussed the effects of these factors on the load that must be carried by the bones. Unfortunately, Thompson did not integrate this information, and, as a result, comes to no general conclusion on the effect of size and different loading situations on limb proportions. Two specific points relative to limb robusticity emerged from his work, however. Firstly, the magnitude of the load that is carried by a limb bone does not necessarily have to increase in direct proportion to the increase in the weight of the animal. If a limb is loaded in bending,

the bending moment is the product of the weight of the animal and the perpendicular distance separating the centre of gravity and the point of analysis on the limb. Depending on the posture of an animal this distance can be varied and, therefore, the bending moment can be varied. Secondly, dynamic loading has the same relative effect of the differential increase of shaft proportions as does static loading.

All of the work until the early 20th century had been primarily theoretical. There had been no attempt to demonstrate on any living population of animals the changes in limb robusticity, shape, distribution of material in the cross-section or the strength of the cortical bone as animals became larger. Therefore, there was no empirical evidence to show which of the loading models was of the greatest significance in determining bone shape, to show whether or not the bones of larger animals were relatively weaker than the bones of smaller animals, or finally, to illustrate the interaction of the variables which combine to give bone its strength in various loading situations.

DuBois-Reymond (1928) was the first of a series of German authors to draw attention to this deficiency and to begin to remedy it. He was primarily concerned with whether or not the bones of larger animals were phsyiologically similar to the bones of smaller animals in relation to body weight. To Galilei's two alternatives for maintaining physiological similarity (the differential increase of the external measurements of the cross-section and the increase in strength of the cortical material) he added a third, the increase in the amount of cortical bone present. He concluded that there was neither a difference in strength of the cortical bone in animals of differing sizes, nor of the amount of cortical bone present. Therefore, in his opinion, the size of the

cross-section accurately reflected the strength of the limb. He compared the body size of the animal (as represented by the sum of the lengths of the vertebral column measured from the skull to the pelvis, the length of the humerus, ulna, femur and tibia) to the limb circumference (as represented by the sum of the circumference of the humerus and the femur) of 23 genera of land vertebrates, 5 genera of sea mammals and 12 genera of birds. Although the data were highly variable he concluded that the model of geometrical similarity could not be rejected. Smaller animals, therefore, necessarily had stronger bones than larger animals. He noted, however, that even the bones of the relatively weak large animals were much stronger than would be necessary if they were only loaded in compression by body weight. He explained this by noting that smaller animals have relatively stronger muscles than larger animals and that the bones of the smaller animals must, therefore, be adapted to the relatively stronger musculature. It is only because large animals are not capable of moving with the same locomotor speed, strength and length of stride as small snimals that the bones have the strength to support the animal.

There are a number of ways in which DuBois-Reymond's analysis can be criticised. Among them are the measurements used, the small numbers of test animals and species used in his strength tests, the small sample size in the tests of relative cortical thickness, the subjective comparison of indices, the disregard of different locomotor patterns and the disregard of the significance of the variation in the data in the robusticity comparisons. However, DuBois-Reymond deserves recognition for being the first to test the hypothesis of physiological similarity on empirical data in reference to skeletal robusticity and to offer a functional explanation for the

relationships he observed.

In 1932 Kreuzer demonstrated that Dubois-Reymond's assumption that the circumference of the cross-section accurately represented the strength of the limb was not universally true. In a well controlled experimental analysis involving an ontogenetic series of guinea pigs he showed that even though the femora became relatively more gracile as the animal grew in size, the relative compressional strength of the bone increased. This increase was shown to be due to an increase in the strength properties of the bone rather than changes in cross-sectional shape or cortical thickness. Kreuzer (1932) also provided some evidence that the strength of cortical bone could be expected to vary between species and, therefore, could not be ignored in any analysis of comparative bone strength.

In addition, Kreuzer (1932) also suggested that the observed increase in the bending strength of the long bones of adult compared with young guinea pigs was more than would be expected according to his interpretation of the law of physiological similarity. He adopted the idea of DuBois-Reymond (1928) and others that the primary force affecting the limbs comes from the muscles and that the force generated by the muscles is proportional to the cross-sectional area of the muscle. Since the ability of the limb to resist the force was also considered to be proportional to its cross-sectional area, Kreuzer suggested that, in this case, geometrical similarity would coincide with physiological similarity. However, the large difference between the predicted strength of an idealised series of bones based on increase according to geometrical similarity, and the experimentally determined strength for a series of real bones, strongly suggested that this hypothesis would not be correct.

Wermel (1935) was also convinced that larger animals had both absolutely and relatively stronger limbs than smaller animals. This opinion was based on his rather naive interpretation of the relationship between the length of the radius of 14 species of mammals and the area of the cross-section of each bone at the midpoint. His data showed that the area of the cross-section in larger animals is relatively larger than that in smaller animals. This positive correlation should not have been interpreted as an indication of greater absolute strength in larger animals, however. The important factor is the strength of the cross-section relative to the load that the limb must carry.

Wermel (1935) also investigated the relationship between the change in shape of the cross-section of a bone with increase in body size. By comparing the length of the radius, which he considered representative of body size, with the section modulus, computed on the dimensions of the cross-section proportionally reduced to a common length, he was able to demonstrate that the cross-sections of larger animals are shaped so as to be stronger than the cross-sections of small animals. Although Wermel's analysis is inconclusive due to the lack of control of the significant variables, it was the first to emphasise the change in shape of the cross-section in robusticity analyses.

In summary, the early work relative to limb robusticity introduced a series of models by which limbs would increase in robusticity to maintain physiological similarity. In addition, it introduced variables other than the size of the cross-section of the limbs and body weight which significantly affect the strength of the limbs and the load they carry. The factors that were thought to affect limb strength were the cross-sectional size and shape and the amount, distribution and strength of the

cortical bone, and the factors affecting the load borne by the bones were thought to be body size, muscle strength and speed of movement, and the manner in which the load was applied (compression, bending, torsion or a combination of these factors). Unfortunately, none of the early analyses were able to control all these variables or to integrate them in a single analysis, and the concept of robusticity and its significance remained confused.

11. 2. B. The Mechanical Significance of the Cross Section of the Long Bones

In Germany analyses of bone form primarily have developed the ideas relating to the mechnical significance of the bone cross-section following on from the work of Rauber (1876, 1877) and Roux (1885, 1895) and the Maximum-Minimum Law. Pauwels is perhaps the best known of these modern authors. In work spanning 20 years from 1948 - 1968 he has redefined the Maximum-Minimum Law to include not only the construction of the individual bones of the skeleton (individual bones are built for their definite stress with maximum material efficiency) but also the construction of the entire post crania of the organism (the stress of the bones through special structure of the post crania is maintained maximally small). In 1948 he illustrated this point with the now classic example of the ilio-tibial tract and its reduction of the bending stress due to body weight on the femur. In addition, he suggested that the muscles could act in a similar fashion and greatly reduce the bending stress resulting from body weight. This is in opposition to many early authors who suggested that muscle action greatly increased stress on bone. In 1950 he further developed this idea and suggested that due to muscle action the bending stress on a long bone was the same regardless of the different positions the bone assumed during locomotion. Therefore, the longitudinal contours of the bone, the distribution of material along the bone

and in the cross-section at various levels in the bone could be arranged for one particular type of stress, achieving the maximum strength with greatest efficiency of material. He illustrated these points with examples of the human tibia and ulna. In later papers he further expanded these points with analyses of the cross section of the human femur in Wormal (1954) as well as pathologically deformed material (1968). Throughout these analyses he emphasises the importance of bending as the force to which the bones must adapt and the use of the section modulus as the most efficient measure of the strength in bending of the cross section of the bone. These ideas were expanded by Kummer (1959-1972) in relation to the human skeleton as well as in relation to the skeletons of other mammals (1959, 1970).

Preuschoft (1961-1979) applied these principles to the post crania of primates with the specific purpose of determining firstly the differences in static stress of individual bones in different types of primate locomotion and, secondly, the differences in form of a bone in the same type of primate locomotion (1969a). From initial work on the post crania of the extant primates, Preuschoft has gone on to analyse post crania of the sub-fossil giant lemuroids of Madagascar (1971a), the Early Pleistocene hominids (1971b) the Miocene apes (1973, and Preuschoft and Weiman 1973) and the Oligocene Fayum primates (1975). Unfortunately, Preuschoft's conclusions in relation to the distribution of cortical bone within the cross section and the resulting strength of the cross section in bending have been confused in his English papers by a translation error from the German. Preuschoft, as the majority of the German school, uses the section modulus to indicate the strength of the cross section in bending. He illustrates strength as measured by the section modulus in the form of a diagram of the cross section with

radiating lines, the length of which indicates the bending strength in that direction (Fig. 11.1). In his English papers he translates the german for section modulus Widerstandsmomenten as moment of resistance. To English speakers this is interpreted as the moment of inertia (Tragheitsmoment in german) which is the total strength of the cross-section and not the strength at the edge. A diagram illustrating the moment of inertia around an irregular bone cross-section would be symmetrical in shape. Because Preuschoft does not give the equations for determination of the section modulus in his English papers, this error has resulted in considerable confusion and frustration in the interpretation of his results, particularly to anthropologists and primatologists who are not generally familiar with mechanical principles.

Where Pauwels, Kummer and Preuschoft have given analyses of specific cross-sections, there are other authors who have dealt with the shape of the cross-section and distribution of cortical bone in more general terms. Knese, Hane and Bierman (1956) on the basis of a theoretical analysis of solid and hollow geometric figures conclude that a hollow section results in the maximum bending strength with a minimum material usage and that a triangular cross-section with a circular hole would provide the most efficient design solution for stress from all directions as well as area for necessary muscle attachment. In addition, on the assumption that the direction of the largest moment of inertia corresponds to the direction of maximum loading they also conclude that, with changing loading on a long bone, there would be a small difference between the maximum and minimum moments of inertia. In quadrupedal mammals they note that the difference in maximum and minimum moments of inertia is small in the hindlimb bones and large in the forelimb bones. They interpret this as a result of difference in function of the forelimbs and the hindlimbs.

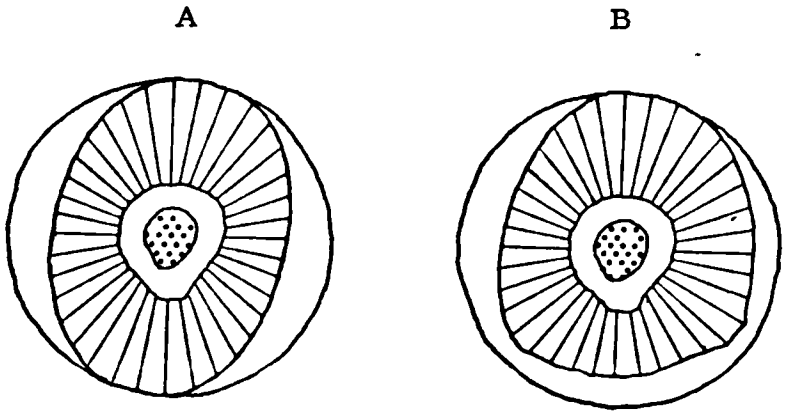

Fig. II. 1. Diagrams of the moment of inertia (A) and the section modulus (B) of the cross section of a long bone. The outer reference circle is drawn with a radius equal to the greatest strength of the cross section. The length of the radiating lines indicates the relative strength of the cross section in the direction of the line. The blank area toward the centre of the diagram is the cross section of the bone. The stippled area in the very centre of the diagram is the medullary cavity of the bone.

Because the forelimbs are the carrying limbs they conclude that the stress would be primarily undirectional and the bone could be weak in directions other than that of the habitual maximum loading. Because the hind limb is a propulsive limb, the uneveness of the ground would create a situation of changing loadings for this limb and would require a smaller difference between the maximum and minimum moments of inertia. In the apes and man the difference between maximum and minimum moments of inertia in the forelimb is less than other mammals, and this would suggest that the loading of forelimb in primates is more uniform in relation to differences in direction than in other mammals. In addition, bipedality in man would allow a great difference between maximum and minimum moments of inertia in the tibia which they interpret to be subject to a uniform anterior posterior bending load, while the small difference between the maximum and minimum moments of inertia in the femur would result from balancing requirements of the orthograde body, which would stress the femur in different directions.

In the English literature, Frankel and Burstein (1965) conclude that a hollow circular cross-section is best adapted to torsion, a hollow square cross-section of varying dimensions is best adapted to bending in the two planes of its sides and that a hollow triangular section is best adapted to both bending and torsion in any arbitrary direction.

Following on from this work there have been a number of mechanical analyses of the human femur and tibia (Amtman, 1971, Kimura, 1974, Lovejoy et al., 1976, and Pizialı, et al., 1976). Lovejoy, et al., (1976) in the analysis of tibial platycnemia in human populations is perhaps most clear in description of methodology of determining the section modulus and polar moments

of inertia. They conclude that the non-platycnemic tibia (eurycnemic), in agreement with Frankel and Burstein (1956), would be equally adapted to all strain inducing modes while the platycnemic tibia would be adapted to situations where anterior posterior and torsional strains were substantially increased over those in the coronal plane.

Although these authors have been concerned with the general mechanical adaptations of the long bones, they have not specifically addressed the problem of the absolute amount of cortical bone in a cross-section relative to external measurements of the cross-section. Currey (1967) approached this problem in the theoretical analysis of the mechanical advantage of exoskeletons in relation to endoskeletons. Considering three modes of failure, rupture, buckling and local buckling in the context of both axial compression and bending, he concluded that in an exoskeleton a very large cross-sectional area in relation to cortical thickness would be advantageous over an endoskeleton under all likely biological situations involving static loading. However, under situations of dynamic loading the advantage of the exoskeleton is decreased and superceded by an endoskeleton. The reason for this is that in impact loading the actual volume of material stress becomes important in resisting localised rupture and buckling. This is particularly important for vertebrates, which are large and active in relation to invertebrates. Although he does not specifically discuss the problem, the actual amount of cortical material in the cross-section is most likely governed by these same principles. For a given amount of cortical material the ideal distribution of bone material is at the greatest possible distance from the centroid of the bone to give maximum strength in bending, and also possibly buckling, while maintaining the necessary

volume to resist crushing and buckling under conditions of impact.

All of these mechanical analyses are based on the hypothesis that bone is a homogenous material. It is well established in the literature that this is not the case (Evans and Lebow, 1951, Dempster and Coleman, 1961, Dempster and Liddicoat, 1952, Evans and Bang, 1967, Knese and Tit schak, 1962, Knese et al., 1954, Amtman and Schmitt, 1968, Amtman, 1968a, b, Evans and Vincentelli, 1969, Currey, 1959). Amtman (1971) has shown that this non-homogeneity enhances, rather than reduces, the mechanical strength of the cross-section based on the calculation of the section modulus. His results show that the bone is relatively stronger just at those sites where the maximal stresses occur and, therefore, the bone would be even stronger in the direction of the highest section modulus than predicted from mechanical analysis, assuming homogenetic of bone strength. However, his results do not indicate that all of the variance in strength in bone material results from mechanical factors. He notes that material strength can result both from varying degrees of mineralisation as well as osteon orientation and orientation of collagen fibres, and suggests that the degree of mineralisation is affected by metabolic factors, as well as structural requirements, while the other strength variables would be primarily affected by mechanical requirements.

This analysis is of considerable importance in the context of lending support to the Maximum-Minimum law and essentially removing the difficult to determine effect of bone material strength as a possibly disruptive variable in mechanical analyses. Instead, it gives confidence and strength predictions based on mechanical analyses of the cross-section which, if anything, err in the direction of too low a prediction.

11. 2. C. The Relationship Between Bone Robusticity and Body Size

Work on limb robusticity subsequent to the early 1930's has been oriented toward the description and explanation of observed robusticity relationships. Unfortunately, not only has the early German work on robusticity and skeletal mechanics gone unrecognised, but also the modern literature relevant to the adaptation of bone to stress has been largely ignored. The modern robusticity analyses are generally based on easy to measure variables that have unproven relationships with the force to which the bone is subjected, or with the ability of the bone to resist that force. This seriously confuses the mechanical, functional or taxonomic significance of the resulting robusticity data. The only exception to this is Jungers and Minns (1979), who deal with the mechanical significance of the cross-section of the femur and tibia in Megaladapis edwardsi. Using computed tomography, they compute the maximum and minimum area moments of inertia for the midshaft section of the femur and tibia in Megaladapis, Indri and Homo, and show that the index of maximum and minimum moments of inertia varies linearly with an index of the anterior-posterior diameter and the medio-lateral diameter of the cross-section. They, therefore, suggest that plausible hypotheses relevant to the mechanical design of the bone cross-section can be made on the basis of classical anthropometric techniques.

This section will cover the literature on the relationship between limb bone robusticity and animal size. It is divided into two subsections. The first reviews the purely descriptive literature on size related robusticity and the second goes into more detail on the literature concerning mechanical models which

have been used to explain the observed robusticity relationships.

11. 2. C. The Allometry of Bone Robusticity

The purely descriptive work on the relationship between robusticity and size has been greatly influenced by Julian Huxley and his work on allometry (1932). Allometry is basically a change in shape that accompanies a change in size (Gould, 1966) and is generally expressed by the power equation

$$y = ax^b$$

where: x = the independent variable

y = the dependent variable

a = a constant

b = the allometric coefficient

For example, using the Galilei-Spencer assumptions that the strength of the limb is proportional to the area of its cross section and the load is proportional to body weight (volume) of the animal, the following relationship would represent a condition of geometrical similarity or isometry

$$y = ax^{2/3}$$

where x = body weight

y = cross section area

2/3 = coefficient of allometry

Therefore, 'y', the area of the cross section would increase according to the two-third's power of 'x', body weight. If this function were plotted, an exponential curve would result (Fig. II.2). This same relationship could be expressed in logarithmic form

$$\log y = \log a + 2/3 \log x$$

When plotted, the curve would be a straight line with a slope of two-third's (Fig. II.3).

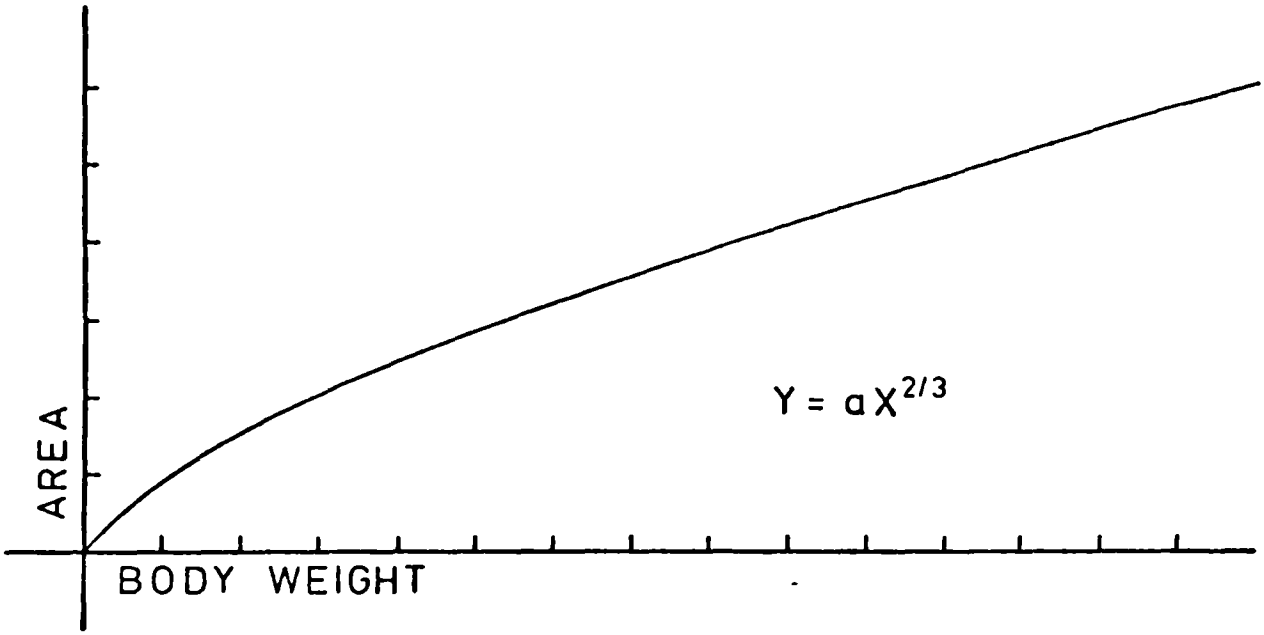

Fig. II.2.

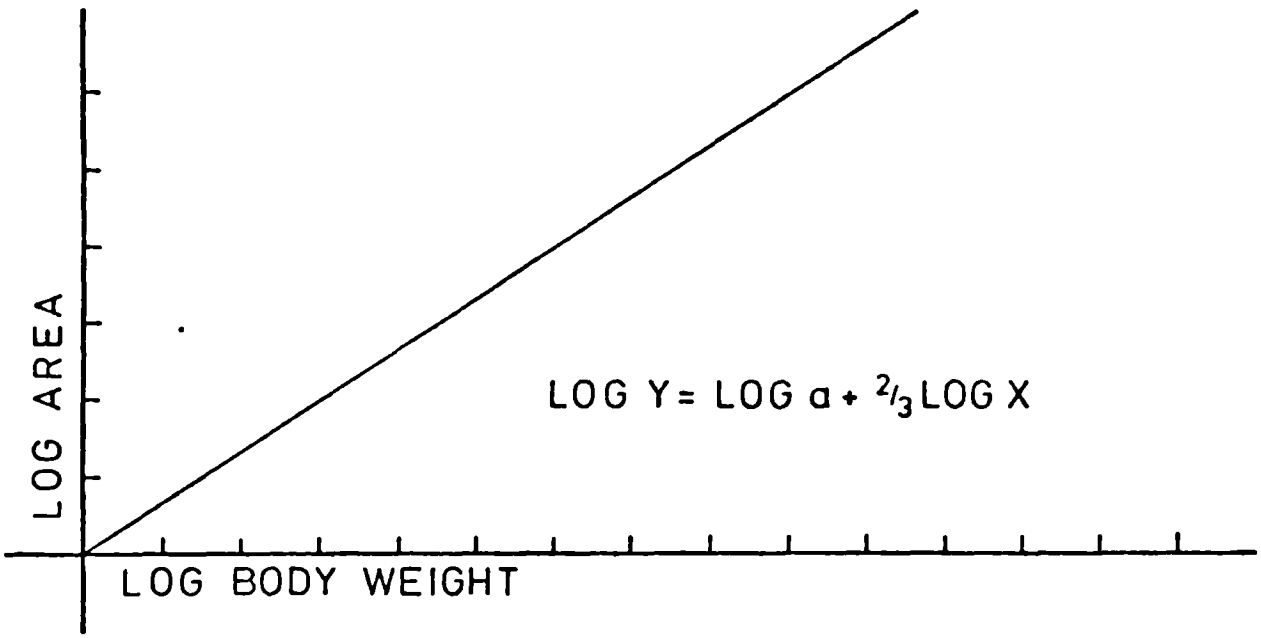

Fig. II.3.

If physiological similarity is to be maintained, the cross section area must increase in direct proportion to the increase in body weight (holding other factors constant). The following relationship would be the theoretical expectation

$$y = x$$

or, $$\log y = \log x$$

This is confusing on initial examination. 'x' and 'y' appear to be increasing isometrically. However, 'x' represents a cubed measurement (body weight or volume) and 'y' represents a squared measurement (cross section area). The equation, therefore, represents the allometric increase of a squared measurement in direct proportion to a cubed measurement. When the logarithmic function is plotted, the curve is a straight line with a slope of unity (Fig. II.4).

Considering linear measurements rather than cross section area and body weight/volume, the following allometric relationships are expected.

$$\log y = 3/2 \log x$$

$$\log x = 2/3 \log y$$

Where x = a linear measurement representing body weight - proportional to the one-third power of body weight

y = a linear measurement representing the cross section - proportional to the one-half power of the cross section area

If physiological similarity is to be maintained, a linear measurement representing the cross section (diameter) will increase in proportion to the three-second's power of the linear measurement representing body weight (Fig. II.5), or the linear measurement representing body weight will increase in proportion to the two-third's power of the linear measurement representing the cross section.

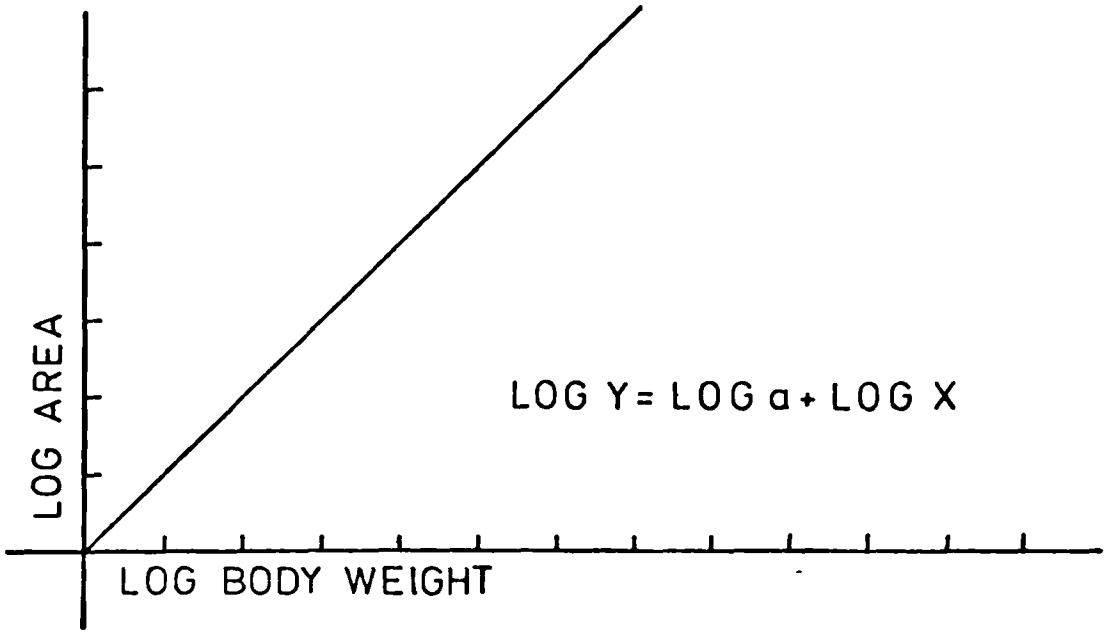

Fig. II.4

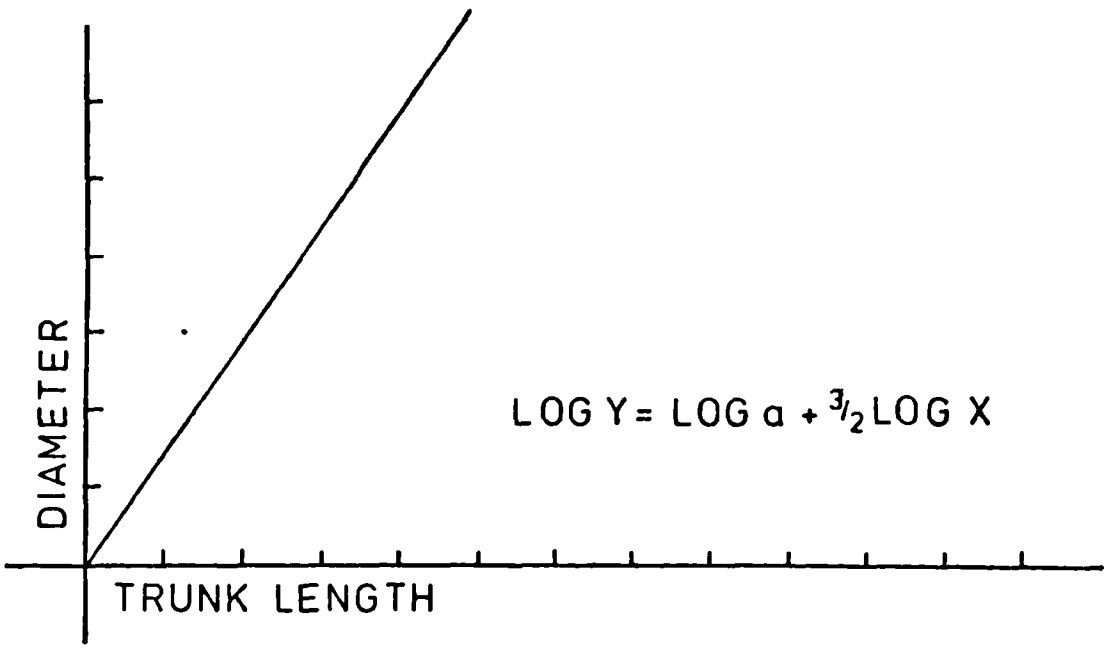

Fig. II.5.

Using empirical data, the coefficient of allometry is determined by fitting a curve to the data points. This is most frequently done with least squares regression analysis on logarithmically transformed data, although this has been criticised on statistical grounds (Teissier, 1948, Kermack and Haldane, 1950, Gould, 1966) and there are other techniques which are more acceptable (see Chapter III).

The allometric equation was first applied to brain weight/body weight relationships in mammals (Snell, 1891, Dubois, 1898, 1914) and birds (Lapique, 1898). Klatt (1919) also applied it to heart/body weight relationships in birds. Huxley (1924) was the first to apply it more generally to the relationship between body proportions in his work on the fiddler crab. He extended it, subsequently, to variables in the dog skull (1927) and the stag beetle (1931). Huxley's well known book Problems of Relative Growth (1932) stimulated diverse applications, as well as criticisms, of the universality of the equation and its biological significance. Hersh (1934) showed that it was applicable to phylogenetically related animals. Huxley, Needham and Lerner (1941) later clearly showed that allometry was equally applicable to the relative growth of variables in ontogenetic analyses as it was to the relationship between variables at one point in time. For clarity of presentation the application of allometry to robusticity will be divided into these three divisions. first, static allometry will be discussed, followed by ontogenetic allometry and phylogenetic allometry.

11. 2. C. 1. (i) Static Allometry of Bone Robusticity

The first application of static allometry to the problem of limb bone robusticity was made by Schlabritsky (1953) on skeletal proportions in chickens. His purpose was to compare the ontogenetic and static allometry of a number of somatic variables with body weight between different sized races of chickens. For 17 birds, belonging to three races, he plotted the average robusticity index (area of the cross-section/length of the bone) for each of the leg and wing bones against average body weight for the race. He concluded that there was a differential increase in robusticity in the heavier race. In addition, he noted that in spite of the inability of the larger race to fly, the relative areas of the cross sections of the humerus and ulna were enlarged by the same measure as were the cross-sectional areas of the femur, tarsometatarsus and the tibiotarsus. He suggested that this might be caused by a pleiotropic gene. Dinnendahl and Krammer (1957) suggested a similar genetic explanation for relationships observed in their ontogenetic data on birds.

More recently, Jolicoeur (1963) analysed the robusticity in the humerus and femur of Martes americana as an illustration of his theory of the multivariate generalisation of allometry. He concluded that the between-sex allometric coefficient was well under the coefficient predicted by the Galilein compression model, but that the within-sex allometric coefficient was not statistically different from this expectation. He suggested that the between-sex deviation might be caused by sexual differences in relative limb length, cross-

sectional shape, cortical strength or general body proportions where the weight of the animal might not consistently vary as the cube of a linear measurement. The fact that the within-sex comparison corresponded to Galilei's prediction suggested to Jolicoeur (1963) that the above factors could more successfully be held constant within the sexes. Jolicoeur's between-sex allometric relationship was computed according to least squares regression analysis and there is no reason, beyond the statistical objections to this technique, to doubt the validity of his results (see Chapter 111). The within-sex coefficient, however, is determined by the ratio of the directional cosines of the variables drawn from the pooled covariance matrix. By comparing these values with the expected values, assuming a multidimensional allometric relationship where the widths of the bones increased as the 3/2 power of the lengths, Jolicoeur showed that there was no significant difference and, therefore, the hypothesis that the widths increased as the 3/2 power of the lengths could not be rejected. However, Hopkins (1966), Sprent (1971) and Corruccini (1976) have since shown that an allometric coefficient derived in this fashion only corresponds to the bivariate allometric coefficient if the logrithmic covariance matrix is of rank one. Therefore, it cannot be assumed that the allometric coefficient for the within-sex comparisons is equal to 3/2 and different from the between-sex relationship. Some difference between the within-sex coefficient and the between-sex coefficient may, in fact, exist, but the proof of this would require additional analysis.

Stahl and Gummerson (1967) have provided the only well controlled analysis of the interspecific allometry of robusticity in primates. Using 35 laboratory animals belonging to five species of New and Old World primates, they determined interspecific allometric coefficients for 81 somatic variables against body weight taken at death. The largest sample size for one species was nine animals and the smallest was two. In spite of the small sample size, the results showed that the long bone midshaft diameters tended to increase more rapidly than would be expected in an isometric situation and that the bone lengths tended to increase at a rate below the isometric expectation, although the specific values for the lengths and widths of the long bones varied considerably. More extensive analyses of these relationships would provide the information necessary to clarify the functional and taxonomic significance of robusticity indices in Primatology. Unfortunately, the potential value of this analysis is severely reduced due to the small sample size both in terms of numbers of individuals and numbers of species.

In another study on the allometry of robusticity, McMahon (1975) measured 118 ungulates, representing 98 different species of Artiodactyles and Perissodactyles. His purpose was to provide data in support of his theory of elastic similarity, which will be discussed in the next section. In the course of this work he made some interesting theoretical and empirical points. He recognised that shape plays a large role in allowing a limb bone to

resist force and, although he corrected for this problem by comparing animals of the same family, he did not provide any evidence to show that this remedy was effective. In addition, he was the first to remark on the possible difference between interspecific and intraspecific allometry with reference to skeletal robusticity. Gould (1971) has discussed this in relation to other factors, but McMahon has specifically suggested that intraspecific allometry in body proportions might approach geometrical similarity, while interspecific allometry would be controlled by the rules of physiological similarity. He indicated that this might be due to either genetic mechanisms or to the fact that bone remodelling mechanisms may require a greater range in body size than exists within a species. Unfortunately, McMahon's data, which samples only one or a few individuals from each of the 98 species, is not sufficient to support or refute this hypothesis.

From this empirical data, McMahon (1975) noted that the robusticity patterns of the ulna and tibia are different in different species. Although he did not expand on it, this is the type of information that would be important in developing functionally or taxonomically significant patterns. He also showed that there is greater diversity in the lengths of distal bones than there is in the lengths of proximal bones in relation to their cross-sections, although he provided no explanation for this. Finally, he observed that the femora scaled closer to isometry than did the other bones studied. The explanation for this is not clear, although McMahon suggested that it might be related to the tendency for larger animals to stand

and move with their limbs held more vertically than smaller animals, and, as a result, reduce the bending moments. No direct evidence was offered in support of this hypothesis, and it is not clear why it should affect the femur more than other limb bones.

In summary, the analyses of static allometry have suggested a series of hypotheses relevant to robusticity relationships. Firstly, there may be a difference in the allometric coefficients within and between sexes and within and between species. These differences apparently result from the differential action of other significant factors which affect either the magnitude of the load borne by the bones or the strength of the bone. Secondly, in inter-specific allometric analyses different bones and different measurements on these bones scale against body weight with different coefficients of allometry. Thirdly, when within-species analyses are compared to between species analyses, or to analyses of higher taxonomic categories, there is some indication that homologous bones may have different allometric coefficients, but the cause of this is unknown. And, fourthly, in certain situations robusticity in some bones may be under the control of pleiotropic genes. Unfortunately, none of these hypotheses has been tested with sufficient control to produce conclusive results.

11. 2. C. 1. (ii) Ontogenetic Allometry of Bone Robusticity

The second application of allometry to problems of robusticity concernes ontogenetic allometry, or the change in robusticity as an animal grows. Kidwell, Gregory and Guilbert (1952) were the first to study allometry of limb bones from this perspective. They studied, among other factors, the relationship in cattle of chest girth, height at hooks, height at withers, and the round (circumference of the leg from the centre of the patella). They found a sexual difference in the allometric equations for these parameters. This indicates a sexual difference in either the growth pattern, the strength of the cortical bone or the loading of the limbs. The round, however, had a higher allometric coefficient than either of the measurements of height in both sexes, indicating an ontogenetic increase in limb robusticity. These relationships are obscured, however, by the complexity of the round measurement, which incorporates the patella, femoral condyles and the skin and muscle surrounding these structures.

The other main ontogenetic study was made by Cock (1963) on two crosses of domesticated chicken. The variables used were shank length, transverse diameter of the shank and body weight of the bird. Cock compared the results of ontogenetic allometry (a regression line fitted to the data for each bird), to cross-sectional allometry (the mean of the measurements for each age category was used to construct the regression line), and to static allometry (the within-group allometry at one period of time). The static analysis showed a negligible correlation between shank length and shank width,

and this indicated to Cock that there were variables other than body size which controlled the growth of the shank length. In addition, Cock demonstrated that there were similar coefficients of allometry for limb length in both the static and cross-sectional analyses, but that this was not true for limb width. The cross-sectional coefficient for limb width was much higher. This difference resulted from the positive correlation between shank width at a given body weight and body weight at a given age. In other words, the higher the body weight at a given age the larger the shank width. Cock noted that this was in agreement with Teissier (1948), who showed algebraically that, given an exact fit to ontogenetic allometry, and assuming the same ontogenetic coefficient in all individuals, a zero correlation between the two variables implied that the coefficient of static allometry was equal to the coefficient of ontogentic allometry, while a positive correlation implied that the coefficient of static allometry was larger than the coefficient of ontogenetic allometry. Although Cock did not attempt to explain this correlation, it might be caused by a difference in the basic strength properties of cortical bone. If there was an increase in strength of the cortical bone in birds with increasing age, a heavier animal at an early age would require a thicker shank than an animal of the same weight at a later age.

In summary, the two ontogenetic studies of robusticity have shown the following relationships. Firstly, there is a sexual difference in the ontogenetic allometric coefficients for limb length and circumference in cattle. Secondly,

age affects the robusticity of a bone in birds at a given body weight, suggesting that there is a change in the strength of cortical bone with age. And, thirdly, there appear to be factors other than body size which control the growth of limbs in birds.

11. 2. C. 1. (iii) Phylogenetic Allometry of Bone Robusticity

The third application of allometry to robusticity concerns phylogenetic allometry, or the application of the allometric equation to phylogenetic data. This type of analysis is similar to that of static allometry, except that the data are paleontological and not contemporary.

Although Hersch (1934) established that phylogenetic data could be allometrically scaled, it was not applied to robusticity until Romer (1948) did so in his discussion of Dimetrodon. For six species of Dimetrodon Romer compared the relative increase of the transverse diameters of the humerus, radius, femur and tibia with cross-sectional area of the vertebral centrum, which is taken as proportional to the weight of the animal. In all cases the allometric coefficient was below the 3/2 predicted by the compression model. Romer explained this by postulating differences in texture of the cortical bone, but there are so many potentially significant variables that it is futile in this conext to attempt to explain the allometric relationship.

A recent major contribution to the phylogenetic allometry of robusticity is Gould's (1967) multivariate analysis of robusticity in pelycosaurian reptiles. This

is not strictly an allometric study, but rather a multivariate confirmation of the allometry of limb robusticity. Gould took as his reference axis the most extreme samples or variables in the data set, and within this framework he carried out two types of analysis. In the first, an R-mode analysis, the degree of association of each variable with the vector composing the reference axis was taken to indicate its degree of functional association. The results confirmed the allometric nature of robusticity by strongly correlating the estimated body weights with bone widths and the estimated body lengths with bone lengths. In the second analysis, a Q-mode analysis, the purpose was to determine the degree of postcranial similarity between species and from this infer a possible explanation for the relationship. If there were only two vectors these could fepresent the size extremes of the data and proportional differences defining these vectors would simply be differences resulting from the allometric effects of size increase or decrease. However, there were three separate vectors represented in the data. When the specific clustering on each of these three vectors were studied in terms of time and paleo-environment they seemed to represent a generalised form from which two specialised locomotor types evolved - a semi-aquatic form and a terrestrial form. Thus, although this analysis does not directly contribute to the understanding of the nature of allometry in postcrania , it does confirm its existence as well as illustrate one way in which the allometry of robusticity can be used to suggest the evolution of different locomotor patterns.

In summary, the analyses which have attempted to study the phylogenetic allometry of robusticity have confirmed its existence, and Gould has gone further and shown how an allometrically based robusticity analysis might be used to indicate the evolution of different locomotor adaptations. The allometry of robusticity used to study the evolution of locomotion is, as yet, an unexploited, but potentially powerful, tool for anthropology.

11. 2. C. 11. Mechanical Models as Explanations for the Allometry of Bone Robusticity

This section will review the literature concerned with the use of mechanical models as explanations for the allometric relationship between robusticity and size. The first mechanical model was Galilei's compression model (1638). This was used to predict the robusticity relationships that would be expected in animals as they increase in size, given the assumptions that in compression the strength of the limb is proportional to the area of its cross section, the force applied to the limb is proportional to the body weight of the animal, and the strength of the cortical bone comprising the cross-section is constant. Spencer (1847) later expanded on this and showed that strength in bending, torsion and tension would produce similar robusticity results. And D'Arcy Thompson (1917) summarised the effects of these factors, as well as the effect of strength in buckling on limb proportions.

The early empirical work on the relationship between robusticity and size (Dubois-Reymond, 1928, Kreuzer, 1932, Wermel, 1935) showed that the predictions of Galilei and Spencers' model were not fulfilled by real data. They suggested a variety of reasons for this changes in cross-sectional shape,

changes in the strength of the cortical bone, changes in the amount of cortical bone, and changes in the application of force. In general, the recent literature, which attempts to provide mechanical explanations for observed robusticity relationships, disregards the complexity of the robusticity relationship and seeks to explain the observed relationship of easy-to-measure variables by one of three mechanical models buckling, elastic stability and bending. These will each be discussed in turn.

11. 2. C. 11. (1) The Buckling Model

Failure in buckling occurs when a column is slender. Under an axial load it will bend at the middle and fail as a result of this bending before it fails in compression. It is, therefore, relatively much weaker than a column made of identical material, but of stouter proportions.

One of the most comprehensive of the analyses concerned with mechanical explanations for robusticity relies on the buckling model to explain, for animals which use their limbs as supporting columns, why the increase in the cross-sectional area is relatively lower in larger animals than required by Galilei and Spencers' model (Ertelt, 1955). Ertelt suggested that small animals, by virtue of their relatively slender limbs, have bones that are subject to failure in buckling, while large animals, with relatively more robust limbs, have bones that are more likely to fail in pure compression. In mechanics a safety factor of 2.5-5 is normally assumed to be necessary for columns loaded in buckling, and a safety factor of 1.5-3 for columns loaded in compression. Ertelt felt that the biological safety factor could be less

in larger animals and, because of this, their limbs could be relatively less robust than predicted by Galilei. This explanation cannot be considered valid, however. Limbs are generally not slender enough to fail as the result of buckling (Wermel, 1935, Alexander, 1968).

Dinnendahl and Krammer (1957) also used the buckling model to explain robusticity relationships in the hindlimb bones of four species of birds. They reported a good correlation when they plotted, for the relatively slender tibiotarsus, the 'Knickzahl' against a combination of skeletal measurements which represented body size. The 'Knickzahl' is the function

$$K = (D^4 - d^4)/l^2$$

where K = Knickzhal
D = the outer diameter of the bone cross-section
d = the inner diameter of the bone cross-section
l = the length of the bone

This function is basically the same as the equation used to determine the maximum load carried by a column loaded in buckling, minus the constants

$$P_{crit} = (n^2 E I)/l^2$$

where P_{crit} = the maximum load which could be supported by a slender column
E = Elastic modulus
I = Area moment of inertia which in a circular or elliptical corss-section is proportional to $(D^4 - d^4)/64$
l = the length of the column/limb
n = a constant which is dependent on the manner in which the ends of the column are fixed

Although the buckling model was not justified by the authors for the tibiotarsus, the bone is very slender and could, in fact, be limited by its

strength in buckling. It is interesting that the relatively more robust femur in the same series of birds scaled equally well with 'Biegezhal', a measure of bending strength, as with "Knickzhal.' In addition, the buckling model as presented is only applicable if the force acts directly along the axis of the column when the column is straight. This is a condition which is probably never fulfilled in animals. If the force lies away from the axis there will also be a bending moment which must be taken into consideration, and a more complicated formula which combines both the stress resulting from compression and that from bending must be applied. Therefore, the 'Knickzhal' cannot be taken to represent the actual strength of buckling.

11. 2. C. 11. (ii) The Elastic Similarity Model

McMahon (1973) suggested that the model of elastic similarity best explains proportions in animals and trees. The model of elastic similarity concerns the ability of a slender cylindrical structure to support its own weight. A slender column is in danger of failing as the result of elastic buckling when the column is so narrow that a small lateral displacement would initiate a progressively increasing bending moment, which the elastic forces of the column could not resist. The equations for maintenance of elastic stability demand that the length of the column is proportional to the two-thirds power of the diameter. This relationship is also constant for models of gravitational self-loading in bending and torsion and, although McMahon does not comment on it, slender proportions are not a requirement under these loading conditions. McMahon concluded that limb bones

should increase in proportion to the two-thirds power of their diameter, no matter if they are loaded in buckling, bending, torsion or a combination of these conditions. He further assumed that the volume of the limb was proportional to the volume or weight of the body or

$$W \propto ld^2$$

where W = body weight
l = length of limb bone
d = diameter of limb bone

Given that the length of the limb bone is proportional to the two-thirds power of its diameter ($l \propto d^{2/3}$), the length of the limb bone would be proportional to the body weight of the animal raised to the $\frac{1}{4}$ power ($l \propto W^{\frac{1}{4}}$), and the diameter of the limb bone would be proportional to the body weight raised to the 3/8 power ($d \propto W^{3/8}$). He compared these predictions with empirical data on ungulates (McMahon (1975), noting a good correspondence he assumed the validity of his model.

There are a number of points in McMahon's argument which can be criticised. Firstly, good correspondence between the predicted and actual relationships only existed for the length and diameter comparisons. The body weight/limb diameter comparisons were supported by Brody's (1945) Holstein cattle analysis, which is primarily an ontogenetic analysis rather than a static analysis. In additon, these comparisons are supplemented by Stahl and Gummersons (1967) primate data, which were based on only 35 individuals, and which showed some degree of deviation from the predictions of the model. Moreover, the correspondence of the limb length/ limb diameter relationship does not, in itself,

necessarily support the elastic similarity model. The same relationship can be predicted by models based on strength in compression or tension, bending, torsion or buckling. Secondly, the predicted relationship between body weight and limb length and limb diameter depends on the untested assumption that the volume of the limb is isometric with body weight. And, thirdly, the loading requirements of the model do not correspond to the actual loading conditions found in animals. The model assumes gravitational self loading, but in animals the loading is a combination of gravitational factors and muscle force. Therefore, neither are the requirements of the model met by the data, nor does the data convincingly support the model.

Alexander (1977) has also recently applied the model of elastic similarity to the allometry of the limbs of eight individuals representing seven species of antelope. He assumed that the body weight/limb length and body weight/limb diameter predictions of the model were correct, and attempted to explain the deviations from the model in bio-mechanical terms. These deviations are found primarily in the diameter and diameter-dependent dimensions of the forelimb, which have allometric coefficients lower than those predicted by the model. Alexander suggested that this occurred as the result of the bending moment increasing at a rate below the increase in the body mass. As D'Arcy-Thompson (1917) earlier indicated, this would occur if the perpendicular distance separating the centre of gravity of the body mass from the midshaft area of the limb decreased

as the animal increased in size. Through a series of calculations idealising the limb proportions and movement, Alexander determined that as an antelope increases in size the angles that the forelimb segments make with the vertical, in mid-step and at maximum speed, are approximately proportional to $M^{-0.04}$, where M represents the body mass. Therefore, as an animal increases in sizes the bending moment would necessarily increase at a slower rate. The diameter of the limb would increase in proportion to the bending moment and not to the body weight and, therefore, would increase at a rate below that predicted by the model of elastic similarity.

Even if the model determining the limb angles is correct, this analysis does not provide an adequate explanation of the allometry of limb robusticity. The variability in Alexander's data, as well as the other data already discussed, suggests that there are more complicated factors than those considered by the model of elastic similarity that influence the length and diameter relationships. In addition, Alexander's argument is only constant if the force to which the limbs are subjected is generally equated with the force resulting from gravitational self loading. It would be illogical to argue that the general limb proportions were determined by a model assuming gravitational self loading and that variations from that model were determined by other loading conditions. There are no data given in support of this assumption. It therefore seems unreasonable to accept elastic similarity as an explanatory

model that needs only to be modified in minor ways.

11. 2. C. 11. (iii) The Bending Model

Strength in bending has also been used as a model to explain differential limb robusticity in animals of different sizes. Preuschoft and Wanmann(1973) developed a theoretical model which argued that larger animals would be expected to have relatively more slender bones than smaller animals, and provided some empirical evidence to support this viewpoint. Their theoretical argument rested on two assumptions. Firstly, the bending moment was proportional to the body weight of the animal. Secondly, the section modulus, a measure of the strength of the cross-section in bending, was proportional to a constant times the diameter of the cross-section cubed. Because body weight can be equated with the cube of a linear measurement representing body size and the strength of the cross-section in bending is proportional to a constant times a linear measurement cubed, Preuschoft and Weinmann concluded that with an increase in size the section modulus would increase at a faster rate than the bending moment. If geometrical similarity was maintained, the bones of larger animals would be relatively stronger than the bones of smaller animals of the same general morphological type. To achieve physiological similarity a larger animal could, therefore, have relatively more slender limbs than a smaller animal.

The main problem with this argument is the assumption that the bending moment is proportional to the body weight of the animal. The moment of a force about a point is defined

as the product of the magnitude of the force and the perpendicular distance from the point to the line of action of the force (Williams and Lissner, 1962). Therefore, in the simplest static analysis, the bending moment affecting a limb would include two components, the body mass of the animal and the perpendicular distance separating the body mass from the point of analysis on the limb. This perpendicular distance would be determined by both the length of the limb and the posture of the body. Preuschoft and Weinmann's model would be correct only if this perpendicular distance were held absolutely constant. There are only two ways to achieve this. As an animal becomes larger both the length of the limb and the posture must be held constant, or the length of the limb and the posture of the body must change simultaneously so as to maintain the same perpendicular distance. Neither of these alternatives are found in their extreme form under natural conditions, and, therefore, the requirements of Preuschoft and Weinmann's model are not fulfilled.

There are also problems with the data that Preuschoft and Weinmann used to support their theoretical conclusions. They compared the average body weight and average relative circumference of the humerus (midshaft circumference/length) for six primate species and attempted to show that this ratio decreased with body size. However, the data for the body weights and for the relative circumference of the humerii were taken from two separate authors, and there is no assurance of correspondence of data. In addition, the six species

used in the analysis differ in both locomotor pattern and general body proportions, and, therefore, the results of this comparison cannot be attributed exclusively to the change in average body mass.

11. 2. C. 11. (iv) Summary

In addition to these rather detailed analyses, which have generally tried, unsuccessfully, to develop models to explain the differential robusticity of limbs in animals of different sizes, there have been passing references in the modern literature to the fact that robusticity does not scale according to Galilei's model. In his phylogenetic analysis of limb robusticity in species of Dimetrodon, Romer (1948) explained the discrepancy by arguing possible differences in bone texture. Schultz (1953) explained it by the general crudity of the model and, in other contexts, suggested that the thickness of the cortical bone, shape of the cross-section of the shaft and the density, strength and elasticity of the bone itself could differentially affect the strength. Kummer (1959), in the course of his analysis of the adaptive significance of the longitudinal curvature of the long bones in mammals, suggested that the larger animals were built to minimise the bending moments on their legs by standing and moving with their legs placed more vertically under the body. Gould (1966) suggested that the deviation from Galilei's model could be explained by 'structural strengthening' and later, (1975), suggested that, in addition, it might be due to larger margins of safety in the bones of smaller animals, or that static considerations of bone strength are not the only determinants of bone

thickness. There have also been attempts to prove that Galilei's model corresponds to empirical fact, as well as to employ the model as if it did correspond to fact. As already mentioned, Jolicoeur's (1963) attempt to prove its validity failed as a result of the methods he used. Rashevsky (1960) employed Galilei's model in support of his general hypothesis that the mass of an animal determines the proportions of its body, and Hill (1950) employed it in his analysis of scaling of animal locomotion.

In summary, none of the mechanical models which have been employed to explain the allometric relationship between robusticity and size can be accepted as correct on the basis of present analysis and evidence. The Galilei-Spencer model, which predicts that the diameter of a bone should increase as the 3/2 power of the cube root of body weight, is unsupported by empirical data. Only if the length of the bone is equated with body weight is there reasonable correspondence betwen the data and the prediction. This, however, is dangerous because within species limb length is not always isometric with body weight and between species limb length is most likely determined by other factors such as locomotion. The buckling model is unsatisfactory because it has not been shown that limb bones are ever slender enough to fail as a result of the buckling. The model of elastic similarity is questionable because it assumes gravitation self loading of the limb under consideration. Although this model offers the best correspondence with the data, there is so much variation in the data, and there is

no theoretical reason to accept the model. It would be unwise at this point to consider elastic similarity a valid explanation for the observed robusticity relationships. And finally, Preuschoft and Weinmann's bending model is unacceptable because it is based on incorrect premises and questionable data.

In addition, all of these models have held potentially significant variables constant. There has not been sufficient analysis of the numerous variables influencing either the strength of the bone or the load it must carry to justify such simplification. Analyses which attempt a generalised mechanical explanation of limb/body size relationships are premature until the effect of variables, such as change in cross-sectional shape, amount and distribution of cortical material, body posture and speed of movement have been studied.

11. 3. The Relationship between Limb Length, Bone Length and Locomotor Patterns in the Higher Primates

Interest in primate limb proportions began with the discovery of anthropoid primates, the substantiation of these animals as the closest relatives of man and the controversy over Darwin's t heory of natural selection. Although limb proportions had been discussed in the early literature on apes and monkeys (Tyson, 1699, Owen, 1859, Vrolik, 1841, Savage and Wyman, 1845, 1847, Duvernoy, 1856), the first well known comparative discussion appears in Thomas Henry Huxley's essay 'The Relations of Man and the Lower Animals' (1864). Huxley's purpose was to provide support for human evolution by natural selection. By comparing limb proportions, as well as other anatomical features, he felt he could demonstrate that man was structurally no further separated from the apes than the apes were from one another. Therefore, if natural selection were to be accepted as the

process by which physical diversification in the animal kingdom arose, there would be no reason why it could not be accepted as the causative factor behind the appearance of man. Huxley recognised the need to correct limb lengths for the effects of body size in his comparisons, and to this end presented all lengths relative to the length of the spinal column. The lengths of the forelimbs and hindlimbs are only described as being without hand and foot respectively, and the spinal column was measured from the upper edge of the atlas to the lower extremity of the sacrum along the anterior curvature. Although similarly indices for the standardisation of limb proportions have been used frequently over the last century, they are not ideal. Body size, itself, may have a direct influence on limb length. Indices of this type do not allow the separation of body size from other causative factors and, therefore, may be ambiguous. The use of indices, however, is not a valid criticism of Huxley in 1864. The method of allometry which successfully separates the effects of body size was not initially employed until 1891 (Snell), and did not come into common usage until the 1930's.

In the last half of the 19th century, Lucae (1865) and Mivart (1867) expanded on Huxley's limited discussion on primate limb proportions. Lucae (1865) included in his analyses not only humans and apes but also a variety of New and Old World monkeys, while Mivart (1867) further expanded the primate sample to 19 genera of higher primate representing four families and 14 genera of prosimian primate representing three families. As Huxley, both of these authors employed the length of the spinal column as a standard of body size. However, they included in their analyses not only the lengths of the complete limbs but also the lengths of the individual bones making up the limbs. Due to lack of available primate material these authors used one specimen to represent each species without regard to sex or age. However, their results are generally comparable to later, more exhaustive, analyses (Schultz, 1930, 1937).

The work of Lucae and Mivart is primarily descriptive in nature. Mollison (1910) added a new dimension to the analyses of primate limb proportions by relating limb proportions to his own classification of locomotor patterns in primate species. Earlier authors had discussed primate locomotion and its relationship to morphology in general terms. Blumenbach, not as commonly believed Cuvier (1817), coined the term Quadrumana to describe non-human primates, while Ray (1693), Gray (1870), and Mivart (1873) emphasised the grasping nature of primate hands and feet. However, both Huxley (1864) and Haeckel (1906) attacked the concept of Quadrumana on morphological grounds. Owen (1859) separated the apes from the remaining primates and classified Hylobates as a brachiator and Gorilla and Pan and Homo as cruriators. During this time, other authors had begun to comment upon variations within the non-brachiating category (Humbolt and Bonplan, 1811, for Ateles, Muller and Schlegel, 1840 for langers, Tennet, 1861, for langers). However, there was no comprehensive classification of Primate locomotor patterns. Mollison (1910) established five major categories of primate locomotion

I. Jumpers (Springer)
   The majority of the prosimians

II. Climbers (Kletterer)
   Cercopithecines
   Macaques

III. Runners (Laufer)
   The ground adapted Cynocephalidea

IV. Brachiators (Hangeler)
   Extreme brachiators - gibbons and orangutan
   Moderate brachiators - chimpanzee and gorilla

V. Bipeds (Ganger)
   Homo

In addition to his interest in locomotor classification, Mollison was concerned by the lack of accurate comparative measurements for not only the nonhuman primates, but also man and also by the lack of statistical analysis of proportional data. He was unaware of the work of Lucae and Mivart and criticised the majority of the 19th and early 20th century work on primate proportions for not describing their measurements and, therefore,

rendering their results useless to other workers (Camper, 1791, Duvernoy, 1856, Humphry, 1858, Ehlers, 1881, Turner, 1886, Eimer, 1901, Fick, 1895, Michaeles, 1903, Sommer, 1906). Consequently, he carefully described his measurements on both cadavors and skeletons, as well as emphasises the use of summary statistics. In total, he studied 266 primate cadavers and 257 skeletons, and listed the measurements and sex of each individual and statistics for each group.

Mollison felt that limb proportions were determined by both affinity and function. However, in his discussions he does not clearly distinguish the effects of these two factors. His results show that locomotor pattern has a large effect on the proportions of the forelimb, both as a whole in relation to the trunk, its parts in relation to the trunk and the parts of the forelimb in relation to each other. The length of the total forelimb relative to the trunk is smallest in the Jumpers, who use their arms only to secure the body once a support has been reached. It is longer in the Climbers, still longer in the Runners and exceedingly long in the Brachiators, which are separated by a wide gap from the other forms. The New World primates parallel the forelimb proportions found in the Old World forms, lacking only the Bipeds.

The relative length of the upper arm parallels the trend of the total forelimb. The shortest upper arm is found in the Jumpers and the longest in the Brachiators, with the Pan having the shortest among this group, followed by Homo sapien, Gorilla, Pongo and Hylobates. There is a wide gap between the brachiators and other categories. The New World primates parallel the limb proportions found among the Old World forms. The relative length of the lower arm follows the same pattern as seen in the upper limb with the one exception that there is no great separation between the brachiators and other locomotor forms.

The brachial index follows a general pattern, the longer the forelimb the higher the brachial index. However, there are some deviations from this which may have specific locomotor

or taxonomic significance. For example, in the New World monkeys, the lower arm is always shorter than the upper arm, although the longest armed forms, Cebus and Ateles, have the indices which approach unity, while the short armed forms have very low indices. In the relatively short armed Lemur the lower arm is equal to, or longer than, the upper, and in the relatively long armed Gorilla and Homo sapiens the index is very low. The cercopithecines are quite variable and in the baboons the lower arm can be relatively longer than in the gibbon. Mollison does not attempt explanation for this variation other than to suggest that in the forelimb the lengthening or shortening of the limb involves primarily the distal segments.

In the hindlimb the length corresponds to the locomotor function. The Jumpers and Bipeds rely on their hindlimbs most for locomotion and, therefore, have relatively longer hindlimbs. The brachiators have the next longest hindlimbs. Mollison explains this as the result of either a shortening of the trunk in these primates or a correlation in growth between the exceedingly long forelimb and the hindlimb (Homotypie).

The gibbon has the longest hindlimb. Mollison emphasised the potential significance of this point for human evolution. This, as well as other anatomical evidence, suggested to early anatomists that man evolved from a gibbon-like ancestor. However, Fleagle (1974) has recently suggested a biomechanical explanation for this lengthening, and other recent information, both biomechanical and anatomical, argues against the hypothesis of a close phylogenetic affinity between man and the gibbons.

To complete the picture Mollison concluded that the Runners have the next shortest hindlimb and that Climbers have the relatively shortest hindlimb of all the primates. In the New World the Cebidae have long hindlimbs in relation to their trunk lengths, while the small Callithrichidae have very short hindlimbs. In a similar fashion Mollison describes the locomotor relationships of the crural and the intermembral indices. His conclusions parallel those for the previous discussed relationships.

In 1914 Martin published the first edition of the Lehrbuch der Anthropologie (followed by the second edition in 1928, and the third edition, revised by Schaller, in 1956 - 1966). Martin not only describes in detail anthropometric measurements on the skeleton as well as the external body, but also discussed limb proportions and robusticity in Homo, as well as selected other primate species. He continues Mollison's interest in evolution and includes the known fossil data at the time in his descriptive summary tables (primarily Neanderthal) but does not discuss the significance of the fossil relationships. Much of the data is drawn from previous references and the results do not differ from those given by Mollison.

This primarily descriptive trend in limb proportions was continued by Adolph Schultz. During his 58 years of professional life (1916 - 1973), Schultz published 144 papers on the growth, variability and pathology of non-human primates. Much of the present knowledge of primate limb proportions is based specifically on his analyses. Although limb proportions are discussed in his earlier papers (1924, 1925, 1926), there are three summary papers which appeared in the 1930's, which provide the comparative data which, not only he, but much of the field, has drawn upon in subsequent years (1930, 1933, 1937). The 1930 and 1937 papers both deal with limb proportions based on the measurement of the skeleton, while the 1933 paper deals with proportions based on external measurements taken on cadavers. Although Schultz claims that measurements of limb segments taken on the skeleton are directly comparable to measurements taken on the cadaver, care must be taken to distinguish the source of the measurements in comparative discussion. When dealing with skeletal measurements the length of the forelimb is taken to be the length of the humerus plus the length of the radius and, correspondingly, the length of the hindlimb is taken as the length of the femur plus the length of the tibia. With cadaver measurements, the length of the forelimb includes the length

of the hand to the end of the most distal digit and the length of the hindlimb includes the distance to the sole of the foot. Because the length of the hand and, to a lesser degree, the distance to the sole of the foot varies independently of the length of the limb (1933), the interpretation of this composite measurement is difficult, it is not directly comparable to the skeletal limb lengths. Schultz clearly describes all of the measurements used in these articles, as well as all of his subsequent work, in his 1929 paper. In general, Schultz's findings in these papers correspond to those of Mivart and Mollison. The majority of Schultz's work is descriptive and he fails to integrate his results, in all but the most general sense, in a functional, taxonomic or evolutionary context. This deficiency may partially be explained by his reliance on indices in the analysis of his data. As Huxley (1932) emphasises, indices do not distinguish between differences in proportion that are dependent solely on differences in body size and those which are dependent on other variables. This confusion obviously results in difficulty in interpretation of the indices. This problem has been increasingly emphasised in recent years by advocates of allometry (Gould, 1966, Preuschoft, 1973, Wood, 1976, Corruccini, 1978).

In the 1930's, however, Schultz could not have been ignorant of the advantages of allometry. It was gaining in popularity in the analysis of verterbrate body proportions (Green and Fekete, 1933 (mouse), Hersch, 1934 (titanotheres) Lerner, 1936, 1937, creeper fowl, Huxley, 1932, primate cranial data supplied by Zuckman (1926)). Although Davenport (1934) suggested that it was not applicable to primate post cranial data, Lumer (1939) using Schultz's own data on anthropoid limb proportions (Schultz, 1930, 1933) illustrated its value in the primate ontogeny. Schultz collaborated with Lumer on the allometric analysis of the ontogeny of limb proportions in Macaca mulatta and in Ateles geoffroyii and Cebus capucinus (Lummer and Schultz, 1941, 1947). Although Lumer (1939) explicitely discussed the advantage of allometry over indices in proportional analyses, neither he nor Schultz continued to

apply this technique to primate post cranial data. It was not until 1967 that the next paper utilising this technique on primate data appeared (Stahl and Gummerson, 1967). This was unfortunate. It was the explicite purpose of Schultz's 1953 paper to distinguish between the effects of body size and other factors on limb robusticity in the primates. Schultz's reliance on indices obscured much of the potential information in his excellent data and allowed him to recognise only gross correlations. The primary hypothesis emerging from this paper is that an increase in limb length does not necessarily require an increase in the circumference of the bone. Limb length is determined primarily by locomotor requirements, and limb girth by body weight. Based on this idea Schultz suggests that the unusual limb robusticity in the fossil lemur, Megaladapis, results from an extreme shortening particularly of its lower limb. He also suggests that shortening of the limbs may be the factor causing the extreme robusticity of the Neaderthal post crania. In addition, he infers body weight and trunk length of the Oreopithecus (1960) based on limb girth, and discusses the significance of the limb proportions of his fossil in locomotor terms.

Application of allometry would have allowed more specific and reliable estimates of the body size, as well as lending credibility to his hypotheses of limb reduction and locomotor pattern by clearly separating the effects of body size, locomotor pattern and taxonomic influence on limb proportions. Hildebrand's analysis of the body proportions in the Canidae (1952) provides an excellent contemporary model of the type of analysis which would have been extremely fruitful for the primates.

These criticisms of Schultz and his approach should not detract from his prolific contribution to primatology, which includes not only the basic collection of primate specimens, but also excellent descriptive monographs relating to the skeletal and soft anatomy of the apes and selected monkey species (see Schultz, 1976, for a complete bibliography of his work).

In 1930, as a part of his description of the primates encountered on a collecting trip to the Gran Chaco, Brazil, Hans Krieg provided a discussion of the relationship between body proportions and locomotor type in New World monkeys. Using Mollison's (1910) five locomotory types Jumpers, Climbers, Runners, Bipeds and Brachiators, he noted that two types, the Runners and Bipeds, were completely lacking from the New World, and that all of the primates belonged to the Climber category, although some showed a greater tendency both in limb proportions and habitual behaviour to Jumping locomotion or to Brachiation. Generally speaking, he viewed the spectrum of locomotor patterns as a trend from Jumping to Brachiation that was brought about by the development of prehensile tail. Why this would be the causative factor is not discussed. Krieg provided data for six genera, Callithrix, Aotus, Callicebus, Cebus, Alouatta and Ateles. He did not give the numbers of each genus studied, and did not describe his measurements other than to say that the reference measurement, the length of the vertebral column from the first thoracic vertebra to the last sacral vertebra, was taken on the dried ligamentous skeleton with a tape measure and that the combined length of the fore and hind limb was used. His results showed that Callithrix, Aotes and Callicebus could be grouped as Jumpers, both in terms of function and body proportions. With the length of the vertebral column standardised to 100, the following proportions resulted

	Forelimb	Hindlimb	Tail
Callithrix	67	87	200
Aotus	68	82	195
Callicebus	61	82	209

Krieg noted the proportional similarity with Colobus, which he considered to be a good Jumper.

	F.l	H.l	Tail
Colobus	68	86	170

Krieg considered Cebus to represent the first stage in the trend toward Brachiation and a prehensile tail, noting on the one hand the relatively undeveloped prehensile features of the tail and on the other the deviation from the proportions of the Springers. In Cebus the front limb is relatively longer in relation to the hindlimb than it is in the Springers. The average length of the limbs (Fl+Hl)/2 is also relatively longer. He noted that this trend is continued in Alouatta. This primate posseses a very muscular prehensile tail that is used as a fifth 'hand' during slow climbing. The trend reaches its extreme form in Ateles, which has developed the prehensile tail into a 'swinging organ.' Krieg noted the similarity in proportions between Ateles and the more extreme Old World gibbon. He suggested that the length of the arms was due to the exclusive role of the arms in Brachiation (as a result of the atrophy of the tail), but does not speculate on the development of Brachiation in the Old World primates in light of the absence of the prehensile tail. He did, however, note that the length of the limbs in Ateles was due to both a rapid postembryonic growth of the long bones and a general shortening of the vertebral column due to both the shortening of the individual vertebral bodies and the loss of vertebrae. The relatively short limbs in the Jumpers was interpreted as the result of the relatively long vertebral column, particularly the greater length of the individual vertebrae.

Priemel (1938) continued Krieg's work with a more detailed analysis of the relationship between post cranial skeletal morphology and locomotor type. His analysis is based on 15 individuals representing 7 genera of New World primates. He employed Krieg's vertebral reference measurement and measurements of individual long bones from Martin (1928). However, these are ambiguous in many cases because of the alternative length measurements provided by Martin. His general proportional conclusions are those of Krieg, with the following elaborations. Firstly, in the lengthening of the forelimb in Ateles the radius plays a greater role than the

humerus. Secondly, the lengthening of the hindlimb in Ateles is interpreted as the result of Mollison's Homotypie and not of a functional cause. Moreover, he interpreted the variation in the average limb length in New World monkeys in the light of Homotypie. Priemel concluded that if the forelimbs in Springers had been shortened from an original length the hindlimbs would have followed, but instead, the legs were much longer. Therefore, the forelimbs could not have been shortened and, therefore, must represent the primitive condition. Needless to say, this line of deduction is based on the untested concept of Homotypie, which is based on the apparent lack of functional reason for hindlimb lengthening in Ateles and Hylobates. Much more concerning ontogeny needs to be studied before this can be taken as fact. And thirdly, Priemel broke away from Krieg's trend of locomotor development in the New World primates and three specialised and distinct locomotor types, the Jumpers, slow prehensile tailed climbers (Alouatta) and prehensile tailed Brachiators, (Ateles). His detailed comparison of locomotor types focused on the Jumpers and prehensiled tailed Brachiators. However, because of the greater number of specialised characteristics found in the Brachiators he considered these to be the derived locomotor type and the Jumpers the original locomotor form.

Washburn (1942) completely ignored the functional implications of limb proportions and was interested in indices only from the point of view of their utility as taxonomic indicators. He compared the intermembral index, the limb length - trunk length indices, the brachial index and the crural index of Macaca irus (16 males and 12 females), Trachypithecus pyrrhus cristatus (12 males and 22 females) and Presbytes rubicunda (19 males and 17 females). The intermembral index was the only index which clearly differentiated the apes from the monkeys. The brachial index, although differentiating the three species, showed a considerable degree of overlap among these species, and, therefore, was not considered to be a good

distinguishing feature. The general utility of the brachial index as a taxonomic indicator was also decreased by its great variability within groups of Old World monkeys and its inability to separate apes from the remaining catarrhines, or to distinguish the two families of Old World monkeys. The crural index was also considered to be of little utility, but as the result of its consistency across taxa. One of the most interesting points emerging from Washburn's analysis is the sexual difference in the index combining limb length and trunk length within species. He demonstrates that the trunk length is longer in the females relative to the body weight than it is in the males. This is due to the longer lumbar region and promontorium-symphysion distance. In addition, he found that the magnitude of the sex difference in weight and trunk height was different in all three groups. Unfortunately, few authors have recognised these problems with trunk length as a constant of comparison.

In the 1950's and early 1960's, increasing fossil evidence relevant to primate post cranial evolution began to appear in the literature (LeGros Clark and Leakey, 1951, LeGros Clark and Thomas, 1951, Napier and Davis, 1959, Schultz, 1960, Zapfe, 1960). During this time the focus of analysis of primate post crania turned to the interpretation of the locomotor capabilities of these fossils, as well as to the general question of the post cranial morphology and locomotor type of the last common ancestor of man and the apes.

11. 4. Limb Length, Bone Length and the Morphology of the Last Common Ancestor of Man and the Apes

From the last half of the 19th century, the roles relating to the course of evolution of man and the higher primates were based primarily on information from comparative anatomy, physiology and embryology. By far the most popular theory saw man descended from an athropoid ape stock (Huxley, 1864, Darwin, 1871, Haeckel, 1866, 1898, 1906, Keith, 1899 - 1934, Miller, 1932). A common locomotor

ancestry of brachiation was suggested by the 20th century authors as an explanation for the similarities in the axial skeleton, viscera and the relatively long arms in relation to trunk length common to both the greater and less apes and to man. These authors felt that adaptations such as the long arms and short legs of the modern pongids were necessarily prerequisite for orthograde posture and bipedal locomotion, and viewed the opposite proportions in man, i.e. the long legs and short forearms, as later adaptations relating to bipedalism. A large amount of the controversy during this period between the Brachiationists and other schools of hominid evolution revolved around the degree of change in the human limb proportions which could have occurred since the last common ancestor of the hominids.

The Brachiationists, with the exception of Morton (1922-35) felt that the last common ancestor was of a relatively large body size and that it was the disadvantage of this large body size which forced the human ancestor to the ground and to a bipedal terrestrial adaptation. Clark (1940), on the basis of the Dryopithecus fontani humerus from Haute Garonne, France, and the Paidopithex femur from Eppelsheim, Germany, suggested that the comparison of the length of the femur and the length of the humerus indicated that the limb proportions of Dryopethicus were by no means so highly specialised for arboreal life as they are in modern apes. Although Clark interpreted the general configuration of the humerus to be closest to Pan, and presumably indicated a brachiating ancestory in the traditional sense, he felt that the lack of arboreal specialisation in the limb proportions indicated that Dryopithecus was a 'ground ape.' In addition, he suggests that the characteristics of the femur indicate that Dryopithecus was much more adept in erect bipedalism than any of the large anthropoid apes. On this basis, he suggests that the human line of evolution took its origin from apes, which were adapted to terrestrial locomotion as was Dryopethicus.

Although Clark does not specifically suggest that this common ancestor was a knuckle walker, Washburn, who from 1950 supported a large bodied common ancestor for man and the apes, later suggested (1967 - 1972) that the last common ancestor knuckle-walked before it became bipedal. This idea has also been supported by Sarich (1971) and Pilbeam (1972 in reference to Miocene drypothecines, and by Napier (1970), Leakey (1971), Kortland (1972), and Robinson (1972) in relation to the robust australopithecines. Tuttle, however, on the basis o his extensive analyses of the hand of the Hominoidea (1967 - 1974) suggested that 'there is no unequivocal direct evidence to support a knuckle-walking stage in hominid evolution' (1974). This conclusion has also been supported by recent analyses of the relevant dryopithecine material and particularly by Susman (1978, 1979), who suggests that the features of the robust australopithecines, which have been interpreted as indicative of a knuckle-walking adaptation, could be better explained in the context of a climbing adaptation.

The hypothesis of a climbing adaptation, and particularly forelimb assisted climbing and suspension during feeding, was originally suggested by Hooton (1946) as an alternative to brachiation to explain the common orthograde adaptations of man and the apes, and has recently gained considerable popularity. Stern (1971a,1976) has suggested it in the course of his work on the comparative myology of the hindlimb of man and the cebids, Fleagle (1976a)has suggested it on the basis of his work on locomotion in the hominids, and Tuttle (1977) has suggested it in relation to the morphology of the hand and forelimb. Tuttle (1977) explicitely suggests that this ancestor was of a relatively small body size, 20 - 30lbs, and of a generalised skeletal morphology. Cartmill and Milton (1977) also support this theory on the basis of the comparison between the lorisiform wrist joint and that of the hominoids.

Although these authors suggest that the common features of orthograde posture shared by the Hominoidea were derived from a climbing adaptation, there were earlier authors who supported a relatively small body size in the last common ancestor and explained the common characteristics variously as resulting from a brachiating small bodied ancestor (Morton, 1922 - 1935, Pilgrim, 1915, Werth, 1928) by extensive parallelisms from more monkey-like ancestors (Boule, 1923, Strauss, 1949). Morton (1926), in particular, employed data on limb proportions in support of his theory of a small bodied brachiating origin of man. He compared the forelimb length (measured from the head of the humerus to the carpal joint) to body length (measured from the first dorsal vertebra to the posterior end of the ischium) in a series of fossil and recent primates and other mammals. Morton felt that long arms relative to body length represented a derived condition in mammalian evolution resulting specifically from tensile stresses encountered in arboreal locomotion. Noting that man was an unusually long armed form, but not as long armed as the anthropoid apes, he concluded that human ancestors must have spent enough time at the brachiating stage to develop increased arm length, but not enough to develop the extremely specialised long arms of the anthropoid apes. He felt, however, that if enough time was spent in brachiating to develop the moderately long arms of man, there would have been enough time to develop the characteristics of the femur and pelvis indicative of gibbon erect arboreal posture which, in his opinion, were essential preadaptations to human terrestrial bipedalism.

There are two other theories of hominoid evolution which deserve mention, if only in historical context. The tarsiod hypothesis of F. W. Jones (1916), and the Dawn Man theory of H. F. Osborn (1927- 1930). Both of these theories postulate a remote divergence between man and the remaining primates and suggest that any similarities between man and the extant pongids are due to extensive parallelism. The brachiationists

of the 1920's spent much of their time and energy defending their point of view against both Jones and Osborn. F. Wood Jones emphasised the differences in the intermembral index of apes and man and the similarity of the index between the tarsiers and man. Based on this, and the morphology of the thumb, he suggested that the tarsier was a direct ancestor of man. The many anatomical similarities pointed out by advocates of the brachiating school were considered to be evolutionary parallelism. Jones' mistake in this theory was his ignorance of the independent features which could cause similar indices and the differences in anatomy and proportions which would exclude this relationship.

Osborn, on the other hand, arguing from his extensive knowledge of mammalian palaeontology, suggested that pre-men, showing a tendency toward intelligent behaviour, bipedality and tool use, would have appeared by the Upper Oligocene. He based this on the early appearance of modern tendencies in the ancestory of other mammalian groups, and suggested that this was also likely in the case of the hominids. In addition, he saw the centre of origin of the hominids in the high plateau and plain regions of Asia. Such an environment, in his opinion, would have provided the conditions for the evolution of the hominid characteristics. He considered the many resemblances between the apes and man to be due to either the very remote common inheritance or to the convergence of the apes toward the human condition. This hypothesis was unacceptable to the brachiationists because of the degree of parallelism it required to explain the many similarities between man and the apes, and has been unsupported by subsequent fossil discoveries.

Therefore, by the late 1940's there were a variety of competing hypotheses for the last common ancestor of man and the apes. Keith and Gregory were the main advocates of the large-bodied brachiator school, Hooton de-emphasised brachiation in favour of climbing as the common locomotor pattern, but still championed large body size, Morton favoured

a small bodied brachiator, Clark suggested a generalised ground ape, Strauss and Boule suggested a more monkey-like ancestor, and Jones and Osborn favoured either tarsier-like ancestors or an essentially hominid-like ancestor in the Oligocene.

Prior to the late 1940's there were only a handful of fossil hominoid post cranial bones known, and for the most part they were either fragmentary or unassociated with other post cranial material from the same individuals. Therefore, little information could be gathered directly from this material relevant to the actual limb proportions of the fossil primates. In addition, the pre-1950 literature relevant to the six non-hominid higher primate species for which post crania existed, was in languages other than English. However, beginning in the late 1940's and early 1950's, fossil primate material, which had been discovered in the earlier decades of this century, as well as newly discovered material, began to be published. This information reinforced the idea of generalised skeleton in the Miocene primates and has been interpreted in various ways to support the brachiating, knuckle-walking and climbing school of hominid evolution. Among the important contributions of this time period are the work of LeGros Clark and Leakey (1951) and LeGros Clark and Thomas (1951), which deals with the hominoid post cranial material from the East African Miocene, Stirton (1951) describing the post cranial of the Late Miocene New World primate Cebupithecia sarmientoi, Napier and Davis (1959) on the forelimb of Proconsul africanus, Zapfe (1960) dealing with Pliopithecus vindobonensis, and Schultz (1960) on the post crania of Oreopithecus bambolii.

LeGros Clark and Leakey (1951) emphasised that the humerus and femur of the Maboko Proconsul were very different from the limbs of the recent Pongidae. Both the humerus and femur were straight and slender, and details of the morphology pointed toward a cercopithecid type of limb skeleton associated with quadrupedal locomotion. The authors emphasised that neither the morphology nor the proportions of the two bones provided any evidence for a brachiating mode of locomotion,

and concluded that the Maboko primate was a generalised running and leaping creature. In connection with LeGros Clark's earlier ideas concerning the evolution of bipedality, LeGros Clark and Leakey (1951) suggest the type of hindlimb found in the Maboko primate and the forelimb of Austriacopithecus weinfurteri would provide a suitable antecedent for both the evolution of the brachiating specialisations of modern large apes (presumably the shortened femur) on the one hand, and of the type of limb structure required for the erect posture characteristic of the Hominidae on the other. They sketch an evolutionary tree in which Pan and Gorilla develop their characteristic brachiating morphology independent from the gibbons and Pongo, and both independent from the line leading to the Hominidae. They see bipedally adapted limbs of the Hominidae evolving by gradual conversion of the primitive limbs found in Proconsul without passing through a brachiating stage. It is interesting that Kern and Strauss (1949) in their discussion of the Plesianthropus transvaalensis distal femur fragment had already pointed out the great similarity in morphology and robusticity between this fragment and the cercopithecine primates and implied a similar course of hominid evolution, although they unfortunately did not compare the fragment to the known Miocene femora. It is also unfortunate that this paper has been interpreted as implying a quadrupedal locomotor pattern for Pleisianthropus, although this is explicitely not the intention. Kern and Strauss emphasise that the cercopithecine characteristics are primitive and these characteristics can be considered to be preadaptations for bipedalism.

Also in 1951 LeGros Clark and Thomas published the monograph on the associated jaws and limbs of Limnopithecus (now Dendropithecus) macinnesi. The conclusions here were similar to those for the Maboko post crania. The bones are primarily straight, slender and cylindrical in character and lacked strong muscle markings. They possess many characteristics which are reminiscent of cercopithecine primates, including the limb proportions. Even though the bones resemble the

gibbons in some details, primarily of the articular surface of the bones, LeGros Clark and Leakey conclude on the evidence of the limb proportions that the arboreal specialisation of the modern gibbons had not yet developed, and that the locomotor pattern was similar to contemporary cercopithecines. They do, however, emphasise the similarity in some morphological details between Dendropithecusand Ateles and suggest Dendropithecus could represent the primitive form from which the gibbons evolved.

In 1951 Stirton also published the short report on the Late Miocene New World skeleton, which he and Savage (1951) had referred to Cebupithecia sarmientoi. Although he does not give a comparative discussion of the morphology, the details provided do not contradict the impression of a generalised and primitive primate skeleton in the Miocene of the New World as well as the Old World.

This picture of a generalised post cranial skeleton among Miocene primates was further supported by the publication of the Proconsul africanus forelimb (Napier and Davis, 1959). In many of the morphological features, the humerus, radius and ulna appear to represent a generalised aboreal quadrupedal primate. However, in such characteristics as the low deltoid insertion, form of the humero-ulnar articulation and horizontal set of the head and the lateral orientation of the convexity of the shaft of the radius, the bones appear to be adapted to a brachiating or arm swinging locomotion. Napier and Davis suggest that Proconsul africanus was a quadruped, in which brachiation, in the most liberal sense of the word, was part of the locomotor pattern. However, they are careful to emphasise that although LeGros Clark and Thomas (1951) arrived at a similar conclusion for Dendropithecusmacinnesi, the pattern of morphology in the two forms is different. Particularly apparent is the difference in the brachial index. Proconsul africanus is characterised by a low brachial index, while Dendropithecus has a higher index indicating humerii and radii of equal length. Napier and Davis (1959) suggest that the low brachial index of Proconsul africanus is a primitive

arboreal feature, and the higher index of Dendropithecus is derived towards the extreme forelimb lengthening found in modern gibbons and siamangs. They believe that a high brachial index occurs mainly in mammals in which lengthening of the whole forelimb has taken place as part of an overall locomotor specialisation. Noting that a low brachial index is typical in the New World primates, they suggest that arboreal life does not necessarily result in the lengthening of the forelimb, and, hence, increase in the brachial index, but do suggest that brachiation results in this specialisation. The relatively low brachial index of Pan and, especially, Gorilla, does not alter their opinion. Pointing out the high intermembral index in these species they suggest that a secondary shortening of the radius has occurred since they both assumed a more terrestrial habitat. They support this hypotheses with the following evidence

1. Pan, which is more arboreal than Gorilla, has a higher index.
2. In the lowland gorilla the total limb length relative to trunk length, the intermembral index and the brachial index all decrease with age.
3. The brachial index of Proconsul africanus is almost identical to Cebupithecia.

The many morphological differences between the Miocene hominoid femora known at this time and the femora of Pan and Gorilla suggest that there are major differences in function. If this is, in fact, true it does not seriously weaken the hypothesis that a low brachial index is the primitive form, but rather casts doubt on the brachiating ancestry (in the sense of gibbons and Pongo) of the extant african apes. What is important with reference to the low brachial index of Proconsul africanus is the definite proof from an associated forelimb that at least one Miocene hominoid in the Old World was characterised by a low brachial index. The only previous example was Austriacopithecus weinfurteri (Ehrenberg, 1938), however, not only is the humerus length estimated from the diaphysis and the radius length from the ulna, but there is no certainty that the two bones are from

the same individual. Based on the two African Miocene hominids, Proconsul africanus and Dendropithecus macinnesi, however, it is certain that already in the Miocene there were at least two distinct brachial patterns.

The three partial skeletons of Pliopithecus vindobonensis (Zapfe, 1960) further support not only the generalised character of the post crania in the Miocene forms, but also the wider occurrence of the high brachial index. Pliopithecus, like the remainder of the Miocene forms lacks the extreme locomotor specialisations of the gibbons and siamangs. Zapfe emphasises the similarity in the limb proportions of Pliopithecus and Papio and Macaca, putting particular emphasis on the virtually equal length of the forelimb and the hindlimb and on the equal length of the humerus and the radius. From this, as well as the ecological position of the fossils, Zapfe concludes that Pliopithecus was not solely arboreal in its locomotion. He extends this conclusion to the other Miocene fossil hominoids and suggests that in the Miocene terrestrial primates were at least more frequent fossils than arboreal primates.

The only Miocene hominoid which, from published reference, does not adhere to the previously discussed generalised quadrupedal pattern is the well known complete skeleton of Oreopithecus bambolii (Schultz, 1960). Although this skeleton is yet to be fully analysed, Schultz (1960) provided a short report on the limb proportions. Schultz suggests that Gorilla is closest to Oreopithecus in its general limb proportions and points out that Gorilla is the most terrestrial of the recent pongids and the least accomplished brachiator. Schultz also emphasises the relatively wide ribcage and pelvis in Oreopithecus, and an apparent reduction of the lumbar vertebra to five. He concludes that Oreopithecus was definitely not a slim, agile, arboreal primate, but rather a relatively slow moving arboreal primate of approximately the size of a chimpanzee.

Schultz's conclusions cannot be uncritically accepted,

however. A footnote in the 1960 paper reports than an x-ray of one of the femora indicates that the bone had been longitudinally compressed, and the length measurement of 243 mm was most likely 20 mm too short. In addition, both examination of the cast of the skeleton in its matrix block as well as photographs of the original reveal that the humerii are of appreciably different lengths. The right appears to be about the same length as the femur, and the left considerably longer and is apparently the one Schultz used for his measurement. Schultz does not mention this discrepancy, and from the available photographs and casts it is not possible to detect which is the least distorted. In view of both the results of the x-ray of the femur and the degree of distortion of the entire skeleton, however, little weight should be placed on the limb proportions for assessing either the locomotor specialisation of this fossil or its phylogenetic affinity until a more detailed analysis is carried out.

The Miocene fossil primate material, with the exception of the Oreopithecus bambolii material, lacks the specialisations in limb and bone proportions recognised in the extant pongids. This, together with the analysis of the morphology of the shafts and joint surfaces, suggests that these fossils did not engage in brachiation, the arboreal locomotor pattern defined at this time for the extant pongids. However, specific features of the post crania, i.e., the brachial proportions in Dendropithecus and the general morphology of the forelimb of Proconsul africanus, suggested that these fossils showed a tendency toward brachiating and lead Napier and Davis (1959) to coin the term 'probrachiation' to describe the locomotor pattern of, particularly, Proconsul africanus. They suggested that the Miocene hominoids were characterised by a complex of characteristics not found in modern forms but resembling the New World semibrachiating primates.

At this time, however, there was little specific information relevant to the locomotor pattern of either semibrachiation or quadrupedalism in the wild, or to the

relationship between post cranial morphology and specific locomotor capability. In the 1960's, however, there are a spate of papers which deal with these topics in view of providing better comparative understanding for the interpretation of the fossil material. Avis (1962) clearly outlines the distinction between brachiating (arm suspension behaviour) in the apes and quadrupedal behaviour in the Old World monkeys, and suggests that man could be best derived from the brachiating group. She is careful to emphasise, however, that the course of human evolution need not have passed through either the gibbon or great ape specialisations. In particular, she emphasises that the large size of the extant pongids would necessarily have resulted in morphological specialisations consistent with a continuing arboreal adaptation, which would not necessarily have also characterised the last common ancestor of man and the pongids.

Her paper has been seminal in relation to later analyses of both brachiation and quadrupedalism in the higher primates. Many of her conclusions relevant to niche utilisation and the biomechanics of arm suspension have been modified. However, her work marked the first attempt to examine in detail the long ingrained concept of brachiation in the apes, and the radical distinction between this form of locomotion and that found in the monkeys.

Erikson (1963) was also interested in establishing the locomotor correlates of brachiating in extant primates and in studying the fossil primates in the light of these variables in order to determine the role brachiating played in hominid evolution.

Erikson was interested in the parallelism in limb proportions between New and Old World brachiators and the variation in proportions in transitional locomotor types. Like others at this time he was interested in establishing the morphological correlates of brachiation in extant primates in order to determine the role brachiation played in hominid

evolution. He measured a total of 1352 skeletons and cadavers of New World primates. However, he relied on Schultz's (1953) data for the comparison between the New and the Old World brachiators. Schultz's material could not be directly combined with Erikson because of differences in measuring technique. For the length of the femur Erikson preferred the distance between the femoral head and the medial condyle to Schultz's measurement which extended from the top of the greater trochanter tothe lateral condyle. In addition, as a measurement of trunk length, Erikson preferred the length of the dried, straightened vertebral column to the distance between the suprasternale and symphysion employed by Schultz and earlier authors. He, therefore, employed his own measurements and data when comparing New World monkeys and Schultz's (1953, table 3, 1956, tables IV, V, VI, VII) when comparing the New and Old World primates.

Erikson used Mollison's locomotor classification which had previously been applied to the New World primates by Krieg (1930), Hiemel (1937). The New World Jumpers were characterised by long, slender trunks, short limbs and hindlimbs longer than the forelimbs. This group included Aotus, Callicebus, Callithrix, Saguines, Cebuilla, Leontideus and Callimico. Erikson notes that the last three show interesting deviations from the group, but does not elaborate. The second group, the Climbers, are medium sized primates with moderately long limbs, shorter trunks and hindlimbs and forelimbs of more equal length. This group included Pithecia, Chiropotes, Cacajao, Saimiri and Cebus. The third group, the brachiators, are characterised by short, inflexible trunks, longer limbs and forelimbs equal to or greater than the hind limbs in length. This group included Alouatta (which was considered marginal), Lagothrix, Brachyteles and Ateles. Erikson noted an overlap in the ranges of the indices used to characterise these groups, and explained this by the transitional locomotor forms. Saimiri, which although included with the Climbers, has some of the habits of Springers,

Alouatta, although included as a brachiator, on detailed analytomical considerations has many characteristics of the Climbers, and Cebus, included among the Climbers, has a prehensile tail and has the highest relative forelimb length and brachial index outside the brachiators.

Erikson also noted that it was possible to detect close parallelisms in limb proportions between New and Old World members of the same locomotor category. For example, Cebus was similar to Macaca, although it has longer limbs than Macaca, while Macaca has a higher intermembral index. Lemur and Aotus are very close in their proportions, and Ateles and Pan are close. Ateles has relatively longer limbs in relation to trunk length, but the intermembral index is similar. Erikson in this context, noted that the size difference would complicate interpretation, but does not pursue the problem. In addition, he noted that the intermembral index is lower in Old World monkeys because, as part time quadrupeds, they have relatively longer hind legs.

In conclusion he noted the difficulty in determining clearly defined locomotor types based on limb proportions and, therefore, the difficulty of devising a system of classification to show the different functional gradiation found particularly in the brachiators. As a result, he felt that the role of brachiation in the Miocene apes and, therefore, its role in hominid evolution, could not be established firmly until more was known of the anatomy, function, behaviour and ecology of contemporary primates. And, indeed, this has been a major focus of interest in recent years, particularly in relation to the more detailed anatomy.

At this time, Ashton and Oxnard, and a number of their colleagues from Birmingham, initiated a far reaching multivariate morphometric study of primate post crania. As Erickson, their purpose was to establish the morphological correlates of the various locomotor types found among modern primates in order to provide a framework within which to interpret the increasing body of fossil primate material.

However, they went beyond Erickson and included in their analyses not only limb proportions but also metrical parameters designed to represent both the topography and the function of the bones of the forelimb and the hindlimb. Early in their analyses they established their own locomotor classification of the primates, which attempted to separate the functions of the forelimb and the hindlimb (Ashton and Oxnard 1964a). They criticised the classification of Mollison (1910), which had been applied in varying forms by the majority of subsequent authors, on the grounds that the function of the forelimb need not necessarily correlate with a single function of the hindlimb in primates. They divided the Anthropoidea on the basis of the degree to which the forelimb is used for suspension and distinguished brachiators, semibrachiators and quadrupeds. Within the semibrachiators and quadrupeds they separated the genera of both the Ceboidea and Cercopithecoidea according to the extent to which leaping occurred.

Their analyses have succeeded in their purpose by separating primate species variously into functional or taxonomic groupings (Ashton and Oxnard 1963, 1964b, Ashton et al. 1965, 1971, 1975, 1976). However, the difficulty with their work, as well as with other multivariate morphometric analyses, is the determination of the significance of the multivariate comparisons. Conflicting results which have been reached by Oxnard and other authors employing multivariate statistics to assess fossil material have pointed out this problem. (Day 1967; Oxnard, 1972, Day 1974, on fossil foot bones, McHenry and Corruccini, 1975a, Oxnard, 1973b; on the proximal and distal parts of the australopithecine forelimb, McHenry and Corruccini, 1975b, Zuckerman et al., 1973, on the pelvis). Multivariate statistical methods are basically elaborate ways of displaying data based on a large number of morphometric variables and arriving at probabilities of similarity of the included groupings (Kowalski, 1973). Problems arise in both the suitability of the statistical techniques (Corruccini, 1978) and the interpretation of the biological significance of the results (Day and Wood, 1968, Corruccini, 1975, 1978, Lovejoy, 1979, Fleagle, 1974, and Day, 1979).

Multivariate statistical analyses enjoyed considerable popularity in the 1960's and early 1970's as a metrical translation of LeGros Clark's concept of the total morphological pattern, which itself was stimulated by the controversy over the taxonomic and phylogenetic placement of the australopithecine material from South Africa. However, because of the difficulties in statistics and in interpretation there has been a tendency toward strict morphological analyses of primate post crania and the information which can be drawn from this type of analysis.

With the decrease in the enchantment over multivariate comparisons, more recent analyses are using multivariate morphometrics as a supplement of qualitatively based functional and morphological analyses, and not relying on them as a technique which, in itself, will provide new and perhaps unsuspected answers to functional questions. The emphasis in this recent analyses has been on the morphology of the joints as indicative of the movement capabilities of the limbs (Morbeck, 1976) away from limb proportions. A particularly important development in the analysis of the relationships between post cranial morphology and locomotor is the reclassification of primate locomotion based on actual observed locomotor behaviour in the wild. Rose (1973a&b) and Fleagle (1976) have emphasised the possible circularity in reasoning that may result from the inference of behavioural capability from morphology in extant primates. The earlier locomotor classifications have tended to rely on the assumed locomotor capabilities of extant primates that was based, at least in part, on the morphology of the post cranial skeleton (Mollison, 1910, Ashton and Oxnard, 1964, Napier and Walker, 1964). Morphology is, therefore, used as the determinant of locomotor classification, whilst, at the same time, is often used to predict locomotor behaviour from the fossil specimen s. This situation has resulted partly from an absence of field studies of primate locomotion, as well as from undue emphasis on the significance of the more spectacular features of primate locomotion, such as acrobatic brachiation in the Hylobatidae, prehensile tailed postures in the Cebidae and vertical clinging

and leaping in the prosimians. The recent tendency is to base classifications on the observ able expressed locomotor behaviour (Morbeck et al. 1979), which involves the complete range of postural and locomotor activities used in travelling, feeding and resting (the total locomotor pattern, Ripley, 1977a&b, or the positional behaviour, Prost, 1965).

The net result of the redefinition of locomotor classification in the higher primates on the basis of positional behaviour (Ripley, 1967, Rose, 1973a&b, Fleagle, 1976), on the basis of the analysis of the relationship between positional behaviour and the environment (Morbeck, 1977a, Ripley, 1977a, 1977b, 1979, Rose, 1977, 1979) and on the basis of positional behaviour and particular functional complexes of the limbs and trunk (Fleagle, 1977a, 1977b, Morbeck et al. 1979) has been to emphasise the locomotor similarities between the apes and the New World semibrachiators and also to emphasise the differences in locomotion between these species and all of the Old World higher primates. The distinguishing criterionn this separation is the use of the forelimb in climbing or suspensory feeding postures and not brachiation.

A number of authors have begun to examine the MEANING of fossil and extant hominoids in the context of a forelimb assisted climbing ancestry, rather than a brachiating ancestry, for this group in general, and for the hominids in particular. Stern (1971) in a detailed comparative analysis of the hindlimb musculature of primates emphasised the similarity between the hindlimb musculature of man and of the New World climbing primate Alouatta. Cartmill and Milton (1977) have emphasised the similarities in the wrist joint between the climbing lorises and the hominoids, and also noted similarities in the axial skeleton and viscera. Tuttle (1975) and Stern (1976) have discussed the morphology of the forelimb within this context. Electromyographic and kinetic analyses also support this distinction. Electromyographic work on the forelimb musculature (Tuttle and Basmajian, 1974a&b, 1977, Tuttle et al., 1972, and Stern et al. 1977) suggests that the same muscles prominently used in arm swinging are

also important in climbing. Stern et al., (1977) particularly emphasise the difference in forelimb musculature use between arm swinging/climbing and pronograde quadrupedalism in the wolly monkey. In addition, Kimura, et al., (1979) have used electromyography to analysize the hindlimb musculature in selected species of monkeys, apes and in man. They document two patterns of hindlimb muscle use in the non-human higher primates. One of these is characteristic of Papio hamadryas and Macaca fuscata, while the second, more human, pattern is characteristic of Ateles, Pan, Gorilla and Hylobates. They have placed these results in a larger kinetic framework, and suggested that the second or more human pattern is associated with a greater differentiation between the use of the hindlimb and the forelimb in body support and propulsion than the first pattern. On this basis, they suggest that the prehuman locomotor pattern would include elements of forelimb suspension and climbing that would emphasise the functional differentiation between the forelimb and the hindlimbs and, in particular, a greater involvement of the hindlimb in propulsion and weight support.

These morphological analyses have recognised specialisations in the post cranial morphology of the extant apes and redefined brachiation as an exclusive locomotor feature of the Hylobatids. Fleagle (1976) suggests that the locomotor features common to the apes can best be explained as adaptations maintained by quadrumanal climbing during feeding activities. Recent analyses of the morphology of Oligocene and Miocene hominoids has suggested that greater similarity is found between these forms and the New World semibrachiating primates.

Although primate limb proportions have not been analysed within this emerging locomotor framework, there is suggestive evidence that they may provide an important source of morphological information in the analysis of locomotor capabilities.

Knusman (1967), in an extensive monograph on the morphology of the humerus, radius and ulna in extant primates, provides a detailed discussion of the morphology of these bones

as well as their proportions and robusticity. Unfortunately, the conclusions drawn from his discussions are confused by his failure to use a constant of body size against which to compare limb length, bone length and bone girth. Even with this criticism, however, he provides interesting support for the hypothesis that brachiation is not a conclusive explanation for limb proportions and robusticity relationships seen in the Hominoidea.

Schultz (1953) suggested that bone length is primarily determined by locomotor pattern, while bone girth is determined by body weight. Based on this premise, brachiators would be characterised by long, slender forelimbs, long to provide the necessary leverage for a forelimb dominated locomotor pattern, and gracile because of the absence of increase in bone girth determined only by the lengthening of the bones. Knussman noted that this pattern is consistent in so far as the specialised brachiating genera of each subfamily of primates (the Hylobatidae among the Hominoidea and Ateles in the Cebidae) are characterised by longer and more gracile forelimb bones than the remaining genera. However, he also notes that this relationship does not hold when the subfamilies themselves are compared. The Hominoidea, which traditionally have been defined as brachiators or modified brachiators, do not have consistently more gracile forelimbs than the Cercopithecidae, which do not engage in suspensory postures.

Knussman also notes that the Miocene fossil primates, Proconsul africanus, Dryopithecus fontani and Austriacopithecus weinfurteri have humerii, which, although gracile, have robusticity indices which fall within the range of the extant Cercopithecidae and the African Pongidae, and do not approximate the indices of Hylobates. In addition, Dendropithecus macinnesi and Pliopithecus vindobonensis which have been interpreted as ancestral to the Hylobatidae, also have humerii considerably more robust than those in the modern Hylobates or Symphalangus. On this basis, he suggests that a robust humerus represents the primitive humeral condition and that this is not consistent with a specialised brachiating ancestry for the Hominoidea.

The brachial index also supports this point. There is considerable variation in the index in the Hominoidea, and the Cercopithecidae and Cebidae fall in the middle of the Hominoidea range. If, as Schultz (1953) suggests, a high index is indicative of a brachiating form of locomotion, these relationships would not support the characteristic form of locomotion of the Hominoidea. In addition, although there is variation in the brachial index of the fossil Hominoidea, none of these specimens are characterised by the extremely high indices observed in Hylobates.

Although Knussman's work fails to isolate the variables which determine the bone robusticity or the brachial index in primates of diverse locomotor patterns, his analysis does emphasise the inconsistency of these proportions in relation to the supposition that brachiation is the integral locomotor feature in either the locomotion of the Hominoidea or the evolution of this group.

11. 5. Limb Length and Bone Length in the Plio-Pleistocene Hominids

In addition to these analyses of limb proportions in Miocene fossil primates and extant primates, there have been speculations over the limb proportions in the Plio-Pleistocene hominids. These analyses are hampered by the lack of associated skeletons for fossils for this time period and have generally relied on length measurements of bones of different individuals (Genet-Varcin, 1966, Coon, 1963, Robinson, 1972, Helmuth, 1968), or indices comprised of measurements which were possible to take on the fragmentary material which was available (Hamilton, 1972, McHenry, 1974, 1978; Robinson, 1972).

Both Genet-Varcin (1966) and Coon (1963) constructed humeral/femoral indices for Australopithecus africanus from the STS 7 proximal humerus and the STS 14 proximal femur. Genet-Varcin's index is 93.7 and Coon's, 96. Both of these fall midway between the mean indices for apes and Homo (Robinson, 1972). Robinson (1972) criticises this approach on the basis of robusticity differences between STS 7 and STS 14 and emphasises the probability that STS 7 is a relatively large

male and STS 14 is a female. Assuming that sexual dimorphism in Australopithecus africanus was similar to that in modern man, Robinson corrects the length of the STS 7 femur to correspond to the femaleSTS 14 skeleton. The corrected humeral/femoral index is 88, which is also midway between apes and Homo, but closer to Homo. In a similar fashion he corrected the length of the STS 14 femur to correspond with STS 7 and arrived at a humeral/femoral index of 89. Robinson concludes, on the basis of this approach, as well as on analysis of the Australopithecus africanus material, that the body proportions in Australopithecus africanus were similar to modern man, with the possible exception that humerus was slightly longer. Robinson also speculates on the possibility that Paranthropus, based on the SW 92 fragment, had a proportionately shorter hindlimb than Australopithecus africanus and, therefore, was more primitive. This assumption is based on a misinterpretation of Schultz (1953) and his theories relating to robusticity. Robinson points out that the magnitude of increase in shaft diameter between Paranthropus and Australopithecus africanus is much greater than the magnitude of increase in femoral head diameter and, therefore, the increase in the 'robusticity' of the shaft could not result solely from increase in body weight. Citing Schultz (1953) Robinson claims that relatively great femoral shaft robusticity in the Pongidae results primarily from increase in body weight. He, therefore, concludes that the relatively great robusticity of the femur shaft of Paranthropus also results primarily from a shortening of the femur. However, when Schultz speaks of robusticity he is referring to the relationship between femur length and femur cross-section. Robinson is using robusticity to refer to a larger shaft diameter in Paranthropus relative to Australopithecus africanus. One of the basic points of Schultz's (1953) analysis is that shortening or lengthening of a bone does not result in a change in cross-section size, and that cross-section size is determined by body weight. Change in the robusticity (femur length divided by femur circumference) comes from shortening or lengthening of the femur in primates of the same body weight. Therefore, Robinson's assertion of

a short femur in Paranthropus cannot be supported.

Helmuth (1969) is much more adventurous than either Genet-Varcin or Robinson, and constructs composite intermembral, crural, brachial and humeral/femoral indices. For the humerus he uses Broom et al.'s (1948) estimate for the length of the STS 7 humerus (300 mm), for the tibia he uses Davis' (1965) measurement of the Olduvai tibia (277 mm), for the femur he uses both Broom et al.'s (1948) estimate for the STS 14 femur (310 mm), and his own estimate based on the width of the epicondyles (390 mm) and for the radius he uses his own estimate of length based on the transverse diameter of the head of the Sterkfontein fragment (Bone, 1955, 203.1 mm). Helmuth's estimates are based on the comparison with a modern human sample. He concludes that the intermembral and humeral/femoral indices are closest to man, if the long femoral length is used, and closest to the macaque, if the shorter estimate is used. In both cases they are far removed from the extant apes. The brachial index is just barely within the range of modern man and far below the range in apes. The crural index based on the 310 mm femoral estimate is consistent with the indices in the rest of the primates, and the index based on the 390 mm estimate is far below the range. Helmuth concludes, on the basis of the similar intermembral and humeral/femoral indices, based on the short femur length, that a quadrupedal, or partially quadrupedal locomotor, pattern cannot be excluded for the australopithecines.

All of these attempts to reconstruct limb proportions from composite material must be treated with caution. The known size variation among the australopithecines and early Homo teeth suggests a considerable variation insize which must also be assumed for the post cranial material and could considerably distort the resulting indices. In additon, the lengths of the majority of the bones used in these analyses are reconstructed from relatively small fragments. In view of the controversy over the length of the STS 14 femur (McHenry 1974, Walker, 1973, Reed & Falk1977, and Helmuth, 1968) the results of these analyses are further suspect.

Up until 1971 the only associated Plio-Pleistocene forelimb and hindlimb material was the TM 1517 distal humerus and talus from Kromdraai (Paranthropus robustus type specimen). Hamilton (1972) compared six indices computed on measurements of the articular surfaces of these two bones with 30 Pan specimens and 70 humans. He concluded that this material falls consistently in the modern human range. McHenry (1974) carried out a similar comparison. By dividing the width of the humeral articular surface by the width of the talar articular surface he derived an index for TM 1517, which fell below the range of variation for these indices in the apes, and above the range of variation in Homo, indicating that TM 1517 had a proportionately longer humerus than would be expected in modern man. Hamilton's analysis was presented as an abstract, so it is not possible to check his analysis in the attempt to reconcile his results with those of McHenry.

As the result of further excavation since 1971, three associated skeletons have been found and published from Koobi Fora and one from Afar. McHenry (1978) has analysed the forelimb and hindlimb proportions and concludes that there are two proportional patterns present. The first is represented by KNM-ER-803 from Ileret area 8A section 08-0103 Loxodonta africanus faunal zone (1.5 Myr) (Homo sp. indet. (Day and Leakey, 1973). McHenry concludes that both visual and metric comparisons of the ulna, radius, femur and tibia show close similarity to Homo. He cites the comparison of the sum of the ulnar anterior-posterior and transverse shaft diameters taken just distal to the ulnar tuberosity, and the sum of the femoral anterior-posterior shaft diameters taken just distal to the lesser trochanter and the estimated long bone lengths in support of this hypothesis.

The second Plio-Pleistocene pattern indicates arms relatively long in comparison with the hindlimbs, and is based on the following specimens

1. KNM-ER-1500 - Koobi Fora area 130 near the KBS tuff in the Mesochoerus faunal zone (Australopithecus Leakey, 1973). McHenry concludes, on the basis of eight ratios, that this skeleton lies outside the human range in most skeletal proportions but usually closer to Homo sapiens.
2. KNM-ER-1503/04 - Koobi Fora area 123 from the KBS, or slightly above (Australopithecus, Leakey 1973). It may possibly not be one individual. McHenry concludes that in some ratios these bones are like man and in others they are not. Comparing the width of the distal articular surface of the humerus and the diameter of the femur head, the fossil is intermediate between apes and Homo. However, comparing the average width of the femur, the fossil is close to the modern human mean. When the lengths of the humerus and femur are reconstructed the humero/femoral index falls between .76 and .90, depending on whether the femur is reconstructed on the modern Homo or on the Pan proportions. Therefore, even when a human reconstruction for the femur is employed the humerus is longer in this fossil than in modern Homo.
3. AL 288-1 - Partial skeleton from the Afar (A. afarensis Johnson and White, 1979). The actual lengths of the humerus and femur show a humerus/femur index of 83.9, which is midway between apes and modern Homo.

The pattern of a relatively long forelimb is also consistent with suggestions made by Leakey (1971) for the long and robust KNM-ER-739 humerus and by Howell and Wood (1974) for the long ulna from the Omo. Although it does seem certain that at least some of the hominids from the Plio-Pleistocene were characterised by a relatively long forelimb. In spite of the uncertainty surrounding the interpretation of some of these measurements, it is not clear whether Homo proportions were the primitive proportions achieved by reduction of the length

of the forelimb/humerus or by the lengthening of the hindlimb/femur. Leakey (1971), Howell and Wood (1974) and Johanson and Taieb (1976) suggest that this is achieved by a shortening of the forelimb. However, there is no concrete evidence to support their assertion other than the long held subjective opinion that human ancestors were brachiators and that long arms are associated with brachiation. As has already been discussed, this impression is not fully supported. One of the aims of the ensuing analysis is to clarify the relationship between forelimb length, hindlimb length and body size in view of providing an answer to the question of primitive limb proportions in the hominids.

11. 6. The Allometry of Primate Limb Length and Bone Length

The major problems throughout the history of study of primate limb proportions and their relation to locomotor or taxonomic categories has been the reliance on indices. Although indices provided standardised means of comparison, they may be influenced by a variety of variables, making interpretation difficult. Allometry, as suggested by Huxley (1932) is a means of facilitating interpretation as well as identifying primitive trends, was first applied to limb proportions in 1967 by Stahl and Gummerson. This was a descriptive study with the purpose of showing that the data could be linearised by the power equation. Maurer (1970/1971), Biegert and Maurer(1972) and Halaczek (1972) however, have applied the technique to the specific purpose of understanding the significance of limb robusticity and proportions in extant and fossil primates.

Using 199 skeletons representing 13 cercopithecoid and hominoid genera, Biegert and Maurer(1972) plotted the ratio of the limb length and trunk length against trunk length. Their measure of trunk length was the 'Rumpskelettlange' or skeletal trunk length, which was determined by summing the ventral height of the thoracic and lumbar verterbra and adding this to the distance from the most ventral cranial point of the body of the sacrum to the most caudal point of the articular surface of the sacrum and this to the distance measured on the illium from the most caudal point of the sacral articular facet to the

most caudal point of the ischium in the axis of the ischium. According to the work of Etter (1969, cited in Biegart and Mauer, 1972), this measure represents on the average 103 - 106% of the ventral trunk length measured on the cadaver. The measurements of the length of the humerus, radius, femur and tibia were taken according to Schultz (1930).

The significant point which emerged from this analysis was that both the length of the forelimb and the length of the hindlimb were positively allometric with body size. Therefore, limb length was not only a function of locomotor adaptation, but also of body size. The larger the primate, the longer would be his limbs relative to body size. In addition, the length of the forelimb increased at a more rapid rate in relation to trunk length than does the length of the hindlimb. Therefore, a larger primate would be expected to have much longer forelimbs relative to both body size and hindlimbs than smaller primates. In other words, merely by virtue of body size a larger primate would be expected to have a higher intermembral index and higher limb/trunk length ratio. The immediately apparent ramification of this relationship is the significance of the length of the forelimb in Pan, Homo and Gorilla and the hindlimb of Pongo, Pan and Gorilla. These fall on a line connecting these genera with the majority of other catarrhine genera, indicating that the limb length is merely a function of size and not of locomotor adaptation. Therefore, on the basis of the evidence of limb proportions neither Homo, Gorilla or Pan need to have experienced a phase of adaptation to a brachiation form of locomotion. In addition, the hindlimbs of Pongo, Pan or Gorilla cannot be considered to be unusually short or atrophied. The forms which are locomotorally specialised are the ones which fall away from the slope characterising the majority of the species. These are the Hylobates, Symphalangus and Pongo for the forelimb length and the Hylobates, Symphalangus and Homo for the hindlimb length. There is a considerable amount of variation around the major allometric slope, however, and it should be expected that a more detailed analysis would reveal

less extreme adaptations in limb proportions characteristic of taxonomic affinity or specific locomotor adaptation.

One of the primary applications of this type of analysis is the determination of the development of extreme locomotor adaptions of brachiation or bipedalism in the fossil record. The problem, of course, in the interpolation of fossils in this type of analysis is the determination of body size. However, Biegert and Maurerconvincingly show that the skeletal trunk length can be predicted with an acceptable average accuracy of 4.3% on the basis of only three vertebra. On this basis they showed that Pliopithecus vindobonesis falls close to the catarrhine tendency in both relative armlength and relative femur length and, therefore, does not show the specialisations of the Hylobates and Symphalangus with which this fossil is often aligned. On the other hand, Oreopithecus bambolii shows forelimbs specialised in length at the magnitude of Pongo, although the femur length falls within the allometric trend for the catarrhines. On the basis of this and the allometric relationships in the pelvis, Biegert and Maurer agree with Strauss (1963) that Oreopithecus had a slow bimanual locomotion similar to Pongo. Unfortunately, Biegert and Maurer do not include any other fossil primates in the analysis, although they do look at the allometry of certain pelvic measurements in both Australopithecus africanus and Australopithecus robustus.

Although this paper is highly significant in terms of the application of allometry, there is one difficulty with the basic assumptions which would significantly alter the results. This is the assumption that the skeletal trunk length is a consistent measure of body size. Schultz (1930) and Erikson (1963) have provided convincing evidence that the trunk length alters with locomotor pattern and Washburn (1942) has shown that it varies with sex. So although the methodology is excellent, the conclusions cannot be accepted as accurate until the relationship between trunk length and body size is analysed.

Irrespective of this criticism, Halaczek (1972) carried the work of Biegert and Maurer(1972) further. He analysed the allometry of the lengths of the long bones of the hindlimb, the circumference of these bones, as well as the size of the joint surfaces and epicondyles in the primates. This was carried out in the context of a morphological analysis of the long bones of the hindlimb in higher primates similar to Knussman's earlier (1967) analysis of the bones of the forelimb. Halaczek's technique was similar to that of Maurer(1970) and Biegert and Maurer(1972). He used raw data instead of a log transformation, fitted the slope by eye and used the skeletal trunk length as the standard of body size. As with these analyses, his results are dependent on the questionable assumption that skeletal trunk length is a consistent with body size across the primates.

Halaczek concludes that the allometry of bone circumference, epiphyses and joint surfaces each show two separate trends across the genera analysed, one composed of Hylobates, Gorilla, Symphalangus, Pan, Homo and Ateles, and the second composed of the small bodied platyrrhines and the Cercopithecoidea. It is suspicious that the species comprising the first group are those which Schultz (1930) and Erickson (1943) have suggested to have a shortened trunk length. Therefore, the two slopes in the relationship of these variables could equally well result from a difference in trunk length as well as a difference in the variables themselves. Halaczek's conclusion that Homo has larger joint surfaces than the remaining primates is of considerable interest, however. Schultz (1930) reports that Homo has not undergone the greatest degree of shortening of the trunk length and is surpassed by Pongo. However, Pongo has smaller joint surfaces relative to trunk length than does Homo. From this it is likely that the large joint surfaces in Homo are a functional correlate of bipedality and represents a specialisation within the primates. Halaczek's point that measurements such as joint surfaces, circumference, etc., must be analysed in relation to body size and not to limb length

is well taken and deserves further research.

In addition to the analysis of extant primates, Halaczek looks at the four genera of Miocene hominoids with preserved hindlimb bones, Proconsul nyanzae, Pliopithecus, Paidopithex and Oreopithecus, as well as Australopithecus. Based on his analyses Proconsul nyanzae, Pliopithecus and Paidopithex are more closely related to the colobines than Hylobates in general morphology. However, again this may be an artefact of trunk shortening in Hylobates and not specifically a closer affinity to the colobines in limb morphology.

Delson et al., (1977) have recently extended Biegart and Maurer (1972) analysis to limb proportions in the australopithecines. Using Biegart and Maurer estimate of trunk length from two vertebra of STS 14 and Robinson's (1972) estimate of the length of STS 14 femur, which is also accepted by McHenry (1974), the femur is slightly longer relative to trunk height than in modern man, and, therefore, falls a good deal above the catarrhine allometric trend. Even if Wolpoff's (1973) shorter estimate of the length of the femur is employed, it is still quite long relative to the allometric trend characterising the catarrhines. They feel that the same relationship is true of Australopithecus robustus. Using Biegart and Mauer's estimate of trunk length based on two vertebra from Swartkrans and Walker's (1973) reconstruction of femur length from Olduvai and East Rudolf specimens, they demonstrated a femur as long relative to the trunk as Robinson's estimate for the Australopithecus africanus femur. When Lovejoy and Heiple's (1970) less secure estimate for the length of a Swartkrans femur is used, the result is also similar to the Australopithecus africanus result. Therefore, on the basis of present data they conclude that the femur in both Australopithecus africanus and Australopithecus robustus had already increased to a length relative to the trunk length that is comparable with modern man. This, in addition to other anatomical evidence, would indicate that the adaptation to bipedal locomotion in both of these forms was

already well advanced. It would also be evidence against Tuttle's suggestion that Australopithecus robustus may have been a knucklewalker (1969).

In summary, over the last 100 years primate limb proportions have been discussed in relation to locomotion of both extant and fossil primates. As the field of primate behaviour and locomotion has developed and the complexity of primate locomotor types recognized, use of data on limb proportions has declined. Erikson (1963) concluded on the basis of his extensive analyses of brachiation in the New and Old World primates that it was not possible to clearly define locomotor types on the basis of limb proportions and emphasised the importance of anatomy as well as functional and behavioural ecology. Advances in these areas have virtually eliminated brachiation as a locomotor category in all but the Hylobatidae, replaced it with a forelimb assisted climbing adaptation and distinguished morphological correlates of the locomotion of both New and Old World higher primates.

However, the differences in limb proportions found in the extant and fossil primates exist, and have not been given adequate explanation. The work on allometry by Biegert and Maurer (1972) provides an indication of the significance of proportions approached through allometry. It is the purpose of this analysis to pursue this problem in relation to primate post cranial material, evaluate the significance of the results and to integrate these results with the relevant data from primate locomotion, morphology, biomechanics and evolution.

III. Materials and Methods

III. Materials and Methods

1. Introduction

The preceding literature review shows that both body weight and the particular locomotor pattern of a primate must be taken into consideration in the evaluation of the mechanical significance of the lengths of the long bones in primates as well as the size and strength of the cross sections of these bones. The pioneering analysis of the allometry of limb length in the higher primates carried out by Biegert and Maurer(1972) was the first published attempt to separate the effects of body size and locomotor pattern in the analysis of the primate post cranial skeleton. It is the objective of this analysis to further explore the interspecific allometric relationships between primate body size and locomotor pattern and those metrical parameters of the long bones which have been used traditionally in indices of limb proportions as well as other parameters which may more accurately represent the strength of the long bones.

The following sections describe the samples, measurements, equipment and statistics employed in the subsequent allometric analyses.

III. 2. The Extant Higher Primate Sample for Skeletal Measurements

Measurements were taken on a total of 272 higher primate skeletons, representing 32 species. This material was gathered from six different skeletal collections and represents wild caught animals wherever possible. In all cases, obviously pathological specimens were avoided. Table III.1 summarises the number of skeletons of each species measured from each collection. In addition, this table provides the primate classification used throughout the analyses. The metrical data gathered from each specimen are presented in Appendix 1.

Table III.2 summarises the locomotor classification employed in the analyses and discussion. The locomotor classification of the quadrupedal higher primates is after Rose (1973b) and the locomotor classification of the non-quadrupedal primates is after Fleagle (1976) and adapted by the author.

Locomotor Category	Included Genera	Included Species	Sample Size		
			Males	Females	Total
Arboreal quadrupedalism - Medium size	Cebus	C. apella	1	1	2
		C. albifrons		1	1
Arboreal quadrupedalism - Large size - Branch Sitting and Walking	Cercocebus	C. albigena	9	8	17
		C. torquatus	4	2	6
	Cercopithecus	C. aethiops	4	6	10
		C. mitis	11	12	23
		C. mona	7		7
		C. neglectus	3	3	6
		C. talapoin	3	5	8
Arboreal quadrupedalism - Large size - Old World Semibrachiation	Colobus	C. badius	7	5	12
		C. guereza	6	5	11
		C. polykomos	4	2	6
	Presbytis	P. obscura	9	13	22
Arboreal quadrupedalism - Large size New World Semibrachiation	Alouatta	A. belzebul		1	1
		A. seniculus	1	1	2
	Ateles	A. paniscus			1*
	Brachyteles	B. arachnoides			1*
	Lagothrix	L. lagothricha	1		1
Part Terrestrial quadrupedalism and part arboreal Quadrupedalism (Branch Sitting and Walking)	Cynopithecus	C. niger		1	1
	Macaca	M. fascicularis	1	2	3
		M. fuscata		1	1
		M. mulatta	1		1
		M. nemestrina		1	1
		M. sylvanus	1	1	2

Table III.1. The sizes of the samples of the extant primate species used in the analysis.

Table III. 1. (continued)

Locomotor Category	Included Genera	Included Species	Sample Size		
			Males	Females	Total
Terrestrial quadrupedalism - Ground Standing And Walking	Papio	P. anubis	3	3	6
		P. cynocephalus	2		2
		P. ursinus	1		1
Brachiation	Hylobates	H. mulleri			6**
Bipedalsim	Homo	H. sapiens - caucasian	10	5	15
		H. sapiens - negro	20	20	40
Knuckle Walking (Pan and Gorilla)	Gorilla	G. gorilla	9	7	16
	Pan	P. paniscus	12	17	29
	Pongo	P. pygmaeus	10	4	14

Table III.2. Locomotor classification of the primates and body weight ranges for each locomotor category.

Locomotor Category	Weight Range (grams)	Included Genera	Included Species	Analyses		
				A	B	C
Arboreal quadrupedalism - Small size - Clawed	156 - 595	Callimico	C. goeldii	*		
		Callithrix	C. argentata	*		
			C. jacchus	*		
		Cebuella	C. pygmaea	*		
		Saguinus	S. fuscicollis	*		
			S. geoffroyi	*		
			S. midas	*		
			S. nigricollis	*		
			S. oedipus	*		
		Leontocebus				
Arboreal quadrupedalism - Medium size ●	603 -3821	Aotus	A. trivirgatus	*		
		Cacajao	C. rubicundus	*		
		Callicebus	C. moloch	*		
		Cebus	C. apella	*	*	*
			C. capucinus	*		
			C. albifrons	*		
			C. nigrivittatus	*		
		Chiropotes	C. satanas	*		
		Pithecia	P. pithecia	*		
		Saimiri	S. oerstedii	*		
			S. sciureus	*		
Arboreal quadrupedalism - Large size - Branch Sitting and Walking ■	2882 - 10183	Cercocebus	C. albigena	*	*	*
			C. galeritus	*		
			C. torquatus	*		
		Cercopithecus	C. aethiops	*	*	*
			C. albogularis	*		
			C. ascanius	*		
			C. cephus	*		
			C. lhoesti	*		
			C. mitis	*	*	*
			C. mona	*	*	*
			C. neglectus	*	*	*
			C. nictitans	*		
			C. pogonias	*		
			C. pygerythrus	*		
			C. diana	*		
			C. talapoin	*	*	*

Table III.2. (continued)

Locomotor Category	Weight Range (grams)	Included Genera	Included Species	Analyses A	B	C
Arboreal quadrupedalism - Large size - Old World Semibrachiation □	3600 - 20334	Colobus	C. badius	*	*	*
			C. guereza	*	*	*
			C. polykomos	*	*	*
			C. verus	*		
		Nasalis	N. larvatus	*		*
		Presbytis	P. obscura	*	*	*
Arboreal quadrupedalism - Large size New World Semibrachiation ▽	5700 - 8890	Alouatta	A. caraya	*		
			A. seniculus	*	*	*
			A. villosa	*		
		Ateles	A. fusciceps	*		
			A. geoffroyi	*		
			A. paniscus	*		*
		Lagothrix	L. lagothricha	*	*	*
Part Terrestrial quadrupedalism and part arboreal quadrupedalism (branch sitting and walking) △	3400 - 21400	Cynopithecus	C. niger	*	*	*
		Macaca	M. speciosa	*		
			M. assamensis	*		
			M. fascicularis	*	*	*
			M. fuscata	*	*	*
			M. mulatta	*	*	*
			M. nemestrina	*	*	*
			M. radiata	*	*	*
			M. sylvanus	*	*	*
			M. sinica	*		
		Mandrillus	M. leucophaeus	*		
			M. sphinx	*		
Terrestrial quadrupedalism - Ground Standing and Walking ▼	9830 - 21800	Erythrocebus	E. patas	*		
		Papio	P. anubis	*	*	*
			P. cynocephalus	*	*	*
			P. hamadryas	*		
			P. papio	*		
			P. ursinus	*		
		Theropithecus	T. gelada	*		

Table III.2. (continued)

Locomotor Category	Weight Range (grams)	Included Genera	Included Species	Analyses		
				A	B	C
Brachiation ○	5228 - 10850	Hylobates	H. agilis	*		
			H. concolor	*		
			H. hoolock	*		*
			H. klossii	*		
			H. lar	*		
			H. moloch	*		*
		Symphalangus	S. syndactylus	*		*
Bipedalism ◇	56700 - 74900	Homo	H. sapiens	*	*	*
Knuckle Walking (Pan and Gorilla) ◆	37750 - 139680	Gorilla	G. gorilla	*	*	*
		Pan	P. paniscus	*		
			P. troglodytes	*	*	*
		Pongo	P. pygmaeus	*	*	*

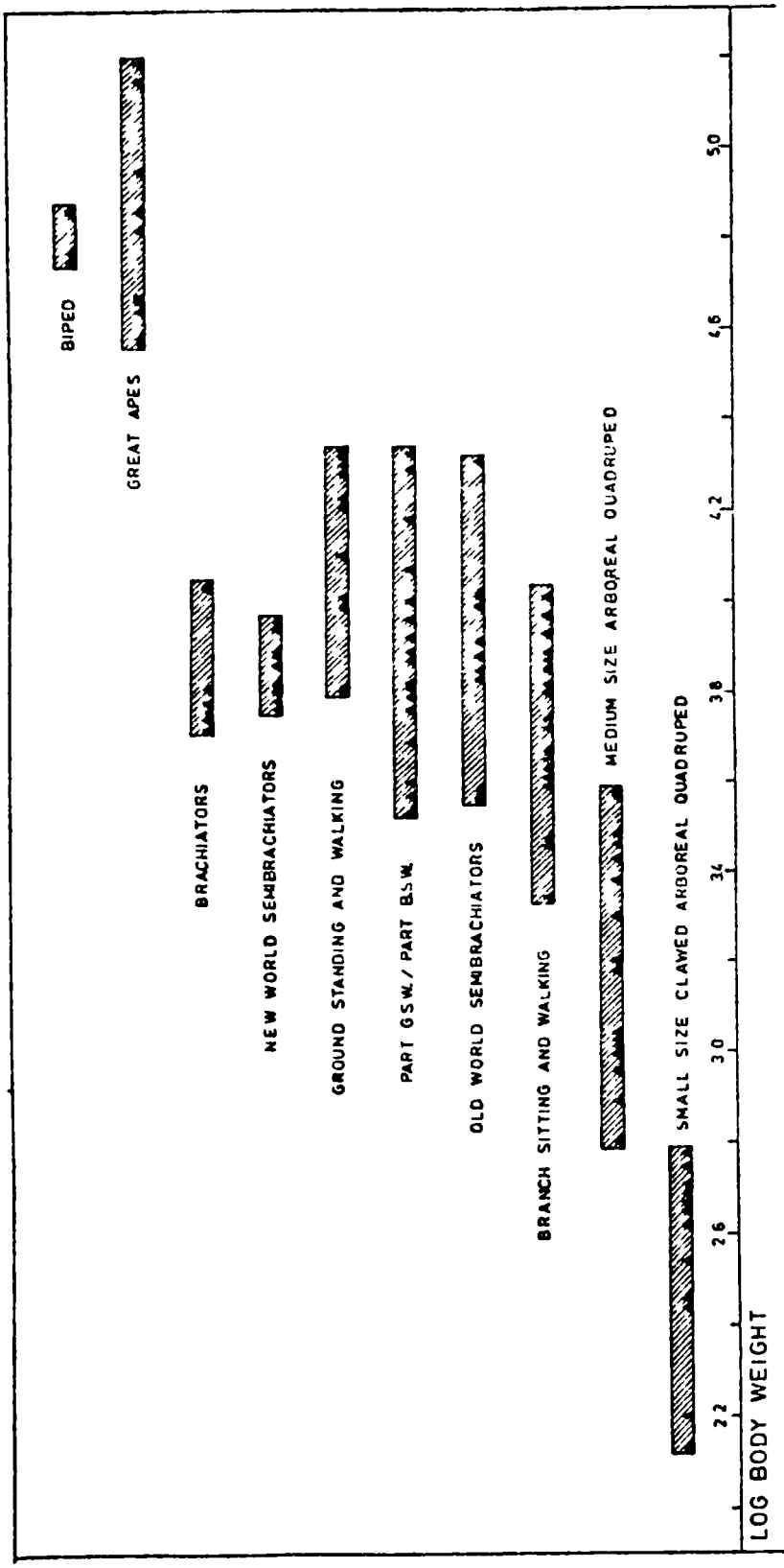

Fig. III.1. The relationship between body weight and locomotor category in the extant higher primates.

These classifications are discussed more fully in Chapter IX. Both Rose and Fleagle base their locomotor classifications on observed positional behaviour of the included primates wherever possible. In addition, they take body size into consideration as an important criteria. Table III.2 includes the body weight ranges for the individual locomotor categories. These body weight ranges are based on the data presented in Section III.4. Figure III.1 summarises these locomotor categories in relation to the body weights of the included primate species. Table III.2 also summarises those species included in the comparison between body weight and locomotor classification (Fig. III.1), those species included in the analyses relevant to the prediction of the body weight of the fossil primates (Chapter VIII) and those species included in the allometric analysis (Chapters IV - VII).

III. 3. The Fossil Primate Sample

Metrical data was collected for 17 fossil primates representing 13 species. In addition, metrical data for a composite reconstruction of the femur of a robust Australopithecus (Section III. 3(k)) was included in the analyses. In all cases, except that of Proconsul sp. indet., these measurements were collected from the literature. The limb bones for Proconsul sp. indet. (Section III. 3 (g)) were measured by the author. Table III.3 summarises the measurements available for each fossil specimen and, in addition, gives the published source for the measurements. Sections III. 3 (a) through III. 3 (o) provide detailed discussions of the measurements for each fossil specimen.

III. 3. (a) Cebupithecia sarmientoi

Cebupithecia sarmientoi is composed of one partial skeleton which was found in 1945 in the Late Miocene La Venta faunal zone in the badlands northeast of Villavaja, Huila, in the upper Magdalenian basin, Colombia, South America. The material was found by Dr. Manuel I. Varon and Sr. Jose Rayo Gonzalez while on a collecting expedition sponsored by the Comision Geologico para Vertebrados, Ministerio de Minas y Petrolaos, Servcio Geologica Nacional

Table III. 3.

POSTCRANIAL MEASUREMENTS FOR THE FOSSIL PRIMATES

	FEL	FECIR	FESD	FETD	HUL	HUCIR	HUSD	HUTD	RAL	FORELIMB	REF.
Cebupithecia sarmientoi					89.3				75.1		15
Proconsul africanus					182 (177 - 187)	34.7*			156	338	1,2*
Pliopithecus vindobonensis Individual I	217	38	11.6	11.7							3
Individual II	206	35	10.5	11.5	173	33.5	10.5	10	181	354	3
Dryopithecus fontani					265		18.6	20.2			4
Paidopithex rehanensus	284	54	16.8	16.0							3
Austriacopithecus weinfurteri					270 - 280 300*	70	21.0	21.0	200		3,5*
Proconsul sp. (Maboko)	285	54	17.2*	16.6*	285	56					6,7*
Dendropithecus macinnesi Speciman I	214 (205 - 226)	40	12.4	12.0	193 (188 - 195)	37.25	10.6	11.0	200 (184 - 206)	393 (375 - 401)	8
Speciman II			10.3	10.0							8
Speciman III			10.0	11.2							8
Mesopithecus pentelici	167.5	40	11.5	13.0	135	32	11	8.5			3
Oreopithecus bambolii	243	79		25	297				282	579	9
KNM-ER-1503/1504	389.8 - 330.6				296.1 - 296.9						10
Walker Reconstruction	360	55.3									11
KNM-ER-739					327.9 ± 6.8						12
KNM-ER-1481	395		22.5	25.3							13
Al-288-1	280				235						14

Table III. 3.

The following abbreviations are used in table III. 3.

FEL	femur length
FECIR	femur circumference
FESD	femur sagittal diameter
FETD	femur transverse diameter
HUL	humerus length
HUCIR	humerus circumference
HUSD	humerus sagittal diameter
HUTD	humerus transverse diameter
RAL	radius length
FORELIMB	forelimb length
REF	reference source for the measurements

The numbers in the reference column correspond to the following references.

1. Napier and Davis (1959)
2. Andrews (per. comm.)
3. Zapfe (1960)
4. Pilbeam and Simons (1971)
5. Ehernberg (1938)
6. Clark and Leakey (1951)
7. Measured by the author
8. Clark and Thomas (1951)
9. Schultz (1960)
10. McHenry (1978)
11. Walker (1973)
12. McHenry (1974)
13. Day et al., (1975)
14. Johanson and Taieb (1976)
15. Stirton (1951)

de Colombia. It was described in 1951 by R. A. Stirton and D. E. Savage, who assigned the specimen to the new taxon Cebupithecus sarmeintoi. In 1951, Stirton pointed out close similarities with the Pithecinae and particularly with Pithecia.

The post crania is composed of a fragmentary scapula, a complete right humerus and left humerus with both ends missing, a left radius complete except for a small section of the shaft, the head of a right radius, both ulnae, miscellaneous metacarpals and phalanges, and fragments of the innominant. In addition, there are the proximal and distal ends of both of the femora and both of the tibiae. The length measurements for the complete long bones (Table III. 3) are after Stirton (1951). There are no midshaft measurements and no attempts to reconstruct the length of the fragmentary femur and tibia. In addition, the exact points of measurement of the humerus and radius are not given.

III. 3. (b) Proconsul africanus

The post cranial material assigned to Proconsul africanus includes part of a left humerus, a radius, a fragment of the ulna, a number of hand bones and miscellaneous bones of the right foot. This material was found in close association with a well preserved mandible, a portion of the right maxilla and premaxilla, fragments of the occipital and a complete right temporal bone. On the basis of the dentition, this material has been assigned to Proconsul africanus (Hopwood) by Napier and Davis (1959). The unerupted M_3 in the mandible and the open epiphysis on the limb bones indicate that the specimen was a young adult.

The material was found by Dr. T. Whitworth in 1951 during the course of a geological survey of Rusinga Island, which is located at the mouth of Kavirondo Gulf, Lake Victoria. The material was found in an unfilled pothole of Miocene age, although possibly slightly younger than

the other Miocene deposits on the island. An Early Miocene date has been generally accepted for the deposits (Simons and Pilbeam, 1965).

(1) Humerus

(a) Length - the left humerus is represented by the proximal three quarters of the bone, the total length of the existing fragment is 132mm. The distal end lacks only the epiphysis of the medial condyle. Napier and Davis (1959) estimate the total length of the bone with reference to the groove for the tendon of latissimus dorsi, which is present just below the break in the fossil fragment. In a comparative sample of 26 juvenile specimens and 42 adult specimens of Pan, Cercopithecus and Papio, the distance from the lower end of the groove to the capitulum makes up 72.3% $\pm$ 1.95% of the total length of the bone measured from the most proximal part of the head to the most distal extension of the capitulum. This results in a total length of 182mm $\pm$ 5mm for the fossil specimen. In the present analysis the length of the humerus is taken as the distance between the most proximal extension of the head and the most distal projection of trochlea (Section III.5). Because the trochlea is slightly projecting in Proconsul africanus, Napier and Davis' mean estimate of the humerus length slightly underestimates the head/trochlear length of the humerus employed in this analysis.

(b) Midshaft Circumference - Napier and Davis (1959) give a robusticity index of 17.2 for this humerus based on the following formula:

$$\text{Robusticity index} = \frac{\text{Circumference at midshaft} \times 1}{\text{total length of shaft}}$$

This results in a circumference of 31.304mm

for the fossil humerus. This is considerably below the measurement of 34.7mm taken on the cast of the humerus (British Museum (Natural History) and confirmed on the original by Peter Andrews (Personal Communication, 1978). This larger measurement is used in the analysis presented here.

(ii) Radius

(a) Length - Although in pieces, the left radius is virtually complete and lacks only the epiphysis of the head. The length of the bone measured from the centre of the proximal metaphysis to the tip of the styloid is 154mm. Napier and Davis (1959) allow 2mm for the missing epiphysis and estimate the total length of the bone to be 156mm.

111 3. (c) Pliopithecus vindobonensis

The post crania of Pliopithecus vindobonensis are composed of the majority of the skeletons of three mature individuals. The material was found together with the cranial and dental fragments in fissure deposits in stone quarry of Neudorf-an-der-March (Nova Ves or Devínská Nová Ves), which is located on the river March on the eastern edge of the Vienna Basin in Czechoslovakia. The material was recovered by Bruno Zapfe in the years before WWII and published by his son Helmuth Zapfe. The extensive monograph which appeared in 1960 was preceded by a series of papers on the geology and fauna of the fissure (Zapfe, 1949, 1950, 1951, 1953, 1954) and preliminary reports on the primate material (Zapfe, 1952, 1958, 1959, 1961, Zapfe and Hurzler, 1957). Based on both the geology and the fauna, the fissure infill is Holvetian or perhaps earliest Torlonian in age.

The measurements in Table III.3 are taken from Zapfe (1960) and are all on the complete bones.

111. 3. (d) Dryopithecus fontanı

A shaft of the humerus lacking both articular ends is the only post cranial bone which has been assigned to the species Dryppithecus fontanı. This bone was found during excavations which produced the type mandibular fragments of D. fontanı. The specimens are from a brick-works at the base of the hill on which the village of Saint Gauden (Haute Garonne), France is located. On the basis of faunal correlations the depo sits are of Sarmartran age (11. 5 - 14. 0 million years) (Pilbeam and Simons, 1971).

Pilbeam and Simons (1971) estimate a total length of 265mm, but do not describe how they arrived at this estimate. The sagittal and transverse diameters are from this same source and are given in Table 111. 3.

111. 3. (e) Paidopithex rhenanus (Pohlig)

Paidopithex rhenanus includes a single femur which was found in 1820 by Schluermacher (Dubois, 1897) in a brickworks in the upper Dinotherium sands near Eppelsheim in Rheinhessen, Germany. There is no other primate material known from this site. Schluermacher's original interpretation of the femur was that it belonged to a 12 year old human, in spite of the fully closed epiphyses. In 1835, Jager assigned it to the primate taxon Anoplotherium aporinum. In 1855-1862 Kaup placed the femur in the genus Dryopithecus which, at that time, had recently been established for the material from St. Gauden, France. Owen (1859) emphasised the similarity of the Paidopithex femur to the femora of Hylobates, however, did not alter the taxonomic designation. Pohlig (1892) was impressed by both the general human form of the femur and the development of a linea aspera. Based on this similarity he suggested that bipedalism was a more frequ ent form of locomotion in this fossil than in modern apes. Pohlig initially assigned the femur to Dryopithecus

(1892), however, in 1895 altered his designation and assigned it to the taxon Paidopithex rhenanus. He was apparently strongly influenced by Zittel (1891-1893). He argued that this femur could not belong to Dryopithecus because it was later in time than the St. Gauden's deposits and because the mandible from St. Gauden was more primitive than the mandibles of modern apes, while the femur, in his mind, was more advanced. Pohlig derived the genus name Paidopithex from Scluermacher's original interpretation for the femur 'young ape.'

Dubois became very excited over Pohlig's hypothesis that the femur was bipedal or, at least, partially bipedal. He felt that it might provide good comparative material for his recently discovered Pithecanthropus erectus femur. Immediately upon his return from Java in 1895 he studied the femur in Darmstadt. He reports his great disappointment in the femur (1895) which, in his opinion, only differed from the femora of modern gibbons in its greater size and, therefore, was not bipedal. In 1897 Dubois referred the specimen to Pliohylobates eppelsheimensis. However, Paidopithex rhenanus has taxonomic precedence and Pohlig's designation was preferred until Simons and Pilbeam's revision of the Dryopithecinea in 1965, when it was returned to Dryopithecus fontani.

In 1900 Schlosser emphasised that the similarity between the Paidopithex femur and the femora of Hylobates did not necessarily disqualify it from being a dryopithecine. He felt that the characteristics of the Paidopithex femur and the femur of Hylobates could be primitive, and in his 1902 paper refers to the femur as Dryopithecus rhenanus. In 1904, with the first X-rays of primate femora, Walkhoff emphasises the similarity in the trabecular orientation between the Paidopithex femur and the femur of the gibbons. In 1926, through a metrical analysis, Giesler showed that it was even closer in its proportions to the siamang. By the 1920's only Abel (1924) continued to suggest that

bipedalism could be possibly inferred from this femur.

The measurements for this femur which are included in Table III. 3 are after Zapfe (1960).

III. 3. (f) Austriacopithecus weinfurteri

Austriacopithecus weinfurteri is composed solely of a slightly damaged right ulna and a right humerus diaphysis. The bones were found in 1931 and 1933 respectively by E. Weinfurter in a sand pit near Klein Hadersdorf, near Poysdorf in north Austria. Based on the microfaunal, the deposits are middle to upper Tortonian. The two bones were first described by Ehernberg in 1937, the ulna as Austriacopithecus weinfurteri and the radius as Austriacopithecus ex. aff. weinfurteri. In 1938 he changed his mind in relation to the humerus and assigned it to the species Austriacopithecus abelii. He justified species separation for the two bones on the grounds that the humerus showed its closest resemblances to the humerus of Pan and the ulna to some of the monkeys. He further argued against the possibility that the bones came from the same individual on the basis that

1. The radius was too short for the estimated length of the humerus.
2. The ulna was too gracile for the humerus.

This opinion did not go unchallenged (Stromer, 1938, Thenius, 1954, 1956, Simonetta, 1957). However, without associated dentition, with such fragmentary material and with a minimum of other fossil primate material with which to compare the specimens, a conclusive decision is impossible. Only the humerus of Dryopithecus fontani was available to Ehrenberg. However, by 1960 and Zapfe's review of the material, additional humerii of Pliopithecus, Dendropithecus, Oreopithecus and Proconsul were available. Zapfe concludes that there is neither evidence for the separation of two species nor is

there strong evidence that the bones could not have come from the same individual. He emphasises that the post crania of all of these species are primitive in comparison with their ape-like dentition. Therefore, mosaic evolution could not be eliminated as a possible explanation. He also emphasises the possibility of a more primitive morphology of the humerus if the joint surfaces were present. In addition, he suggests a shorter estimate for the length of the humerus which would bring the brachial index within the range of Homo and Gorilla and, therefore, not exclude the possibility that the bones were from the same individual. He also believes that the very gracile ulna in relation to the humerus is not strong evidence against this hypothesis. The material is not assigned to Dryopithecus because of the essential differences between the St. Gauden humerus and this humerus which primarily concerns a greater robusticity in this shaft and a different cross section shape.

The humerus is represented by the diaphysis lacking the head and the distal joint surface including b the medial and lateral epicondyles. A large part of the Crista supinatoria is present, however, as well as almost one half of the olecranon fossa. Zapfe estimated the total length of the humerus on the basis of the ratio of the distance between the proximal edge of the olecranon fossa and the dividing point between deltoid tuberosity and Crista tuberculi majoris. He related this to the total humeral length based on Pan and Homo as a comparative sample. The estimated length is 270 - 280mm. Zapfe believes that this estimate can be independently supported by comparing the ulna to the humerus. If the ulna is fitted into the olecranon fossa of the humerus, the missing part of the humerus could not exceed 30mm measured from the distal fracture of the humerus to the coronoid process of the ulna. According to Zapfe, this would leave 64 - 74 mm for the missing proximal fragment or 23 - 26% of the

estimated length. In most higher primates, with the exception of Ateles and Hylobates, the intertubercular sulcus makes up 20 - 35% of the shaft. Because the sulcus is missing on the fragment, according to this reasoning, 20 - 35% of the shaft could be missing. Zapfe believes that the 23 - 26% estimated for the missing section is in good agreement with this. However, there is a problem with Zapfe's figures. According to the actual measurement given in the monograph, Zapfe's percentages are too high. They should read 22 - 23.7%. In addition, Zapfe's line of reasoning does not disprove Ehrenberg's original length estimate for this bone ($\pm$ 300mm). This estimate would leave 27.23% of the bone missing and, in fact, falls closer to the mean percentage estimate for the length of the intertubercular sulcus and, therefore, may be a more reasonable estimate of actual length. However, all that can be definitely concluded is that on the above reasoning neither of the estimates can be rejected as improbable.

The estimate for the length of the ulna is more secure. The ulna is virtually complete except for the absence of the distal diaphysis. Zapfe notes that in all higher primates except Hylobates, Pongo and Ateles, the distal ephiphysis makes up to 5 - 6% of the total length. Based on this reasoning, the total bone length would be 219.4 - 221.8mm. This agrees well with Ehrenberg's estimated length of 220mm. The length of the missing radius can be estimated to be $\pm$ 200mm based on the distance between the incisura radialis and the distal end of the ulna. Bone measurements are given in Table III.3.

III 3. (g) Proconsul sp. indet.

The post cranial material assigned to Proconsul sp. indet. was collected in 1933 by Archdeacon Owen on

Maboko Island in the Kavirondo Gulf of Lake Victoria. It includes a right femur lacking the head, greater trochanter and most of the distal epiphysis, the upper extremity and shaft of a left femur, the shaft of a left humerus lacking both articular ends and part of a right clavicle. LeGros Clark and Leakey (1951) report that the material most likely comes from the same individual although there appears to be no direct evidence to support this conclusion. By process of elimination they assign the material to Proconsul sp. indet. Mesopithecus and Limnopithecus (now Dendropithecus) were too small in size to receive this material and the only other available genus, Sivapithecus africanus, was considered too rare to be a likely choice.

The deposits at Maboko are younger than the majority of the East African Miocene sites, and are now thought to be of Middle Miocene age (Andrews, personal comm.).

(1) Femur

(a) Length - the length of the femur is estimated at 285 $\pm$ 15mm (LeGros Clark and Leakey, 1951). This estimate is based on the right femur shaft, after the head and neck had been reconstructed according to the existing head and neck of the left femur. The 15mm error allows for the uncertainty in the reconstruction of the distal end of the bone. It is not clear if the estimated length of the femur is the functional length of the femur (Section III.5). However, LeGros Clark and Leakey do not mention reconstruction of the greater trochanter which would be necessary for the greater trochanter/medial condyle length. Their estimate has been checked against the newly cleaned and reconstructed specimen and does appear to be an accurate estimate of the functional femur length.

(b) Midshaft Circumference - LeGros Clark and Leakey (1951) give the following midshaft measurements ·

Sagittal diameter - 18mm

Transverse diameter - 17mm

Measurements taken by the author at midshaft are

Sagittal diameter - 17.2mm

Transverse diameter - 16.6mm

Circumference - 54mm

(2) Humerus

(a) Length - the left humerus shaft is broken by transverse fractures into five pieces. The pieces fit together accurately, however, there is some post-mortem distortion of the shaft and it angles laterally in its distal quarter. LeGros Clark and Leakey estimate the length to be 280mm. This is a subjective estimate based on the presence of the upper margin of the olecranon fossa at the distal end and the incipient widening of the shaft at its proximal end.

(b) Midshaft Dimensions - the following midshaft measurements were taken by the author on the original ·

Sagittal diameter - 18.45mm

Transverse diameter - 18.mm

Circumference - 56mm

111. 3. (h) Dendropithecus macinnesi

The post crania of Dendropithecus macinnesi include bones of both the forelimb and hindlimb. From the forelimb there is a right humerus which is complete to the base of the lesser tuberosity, the proximal half of a right radius and a fragment of an ulna. From the hindlimb there are four incomplete femur shafts, a femur head, a tibia shaft, a fragment of the fibula, an incomplete

calc neum and part of a talus. All of the postcrania were found closely associated in one block with a right immature maxilla, a palate and upper dentition of a young adult and two isolated teeth. Immediately adjacent was a mandibular fragment belonging to the same individual as the adult palate and a fragment of an immature mandible. The dentition belongs to four individuals, as do the limb bones. On the basis of dentition and close association the entire collection has been referred to Limnopithecus macinnesi by LeGros Clark and Leakey (1951) and to Dendropithecus macinnesi by Andrews and Simons (1978).

The material was discovered by L. S. B Leakey in 1948 on Rusinga Island. The deposits are of Lower Miocene age. The specimens are desxribed in LeGros Clark and Leakey (1951).

(1) Forelimb -

The forelimb material is composed of most of a right humerus, the proximal half of a right radius and a fragment of a right ulna. On the basis of their proximity in the deposits, size and articular apposition they most likely belong to one individual.

(a) Humerus - the humerus is complete to the base of the head of the lesser tuberosity. LeGros Clark and Leakey estimate the length on the basis of the ratio of the following three measurements to the total length of the bone. The reference sample was composed of eight specimens representing the genera Hylobates, Symphalangus and Ateles.

(i) The length measured to the upper end of the posterior aspect of the neck of the humerus where it approximates the lower margin of the articular head.

(ii) The length measured to the midpoint of the base of the lesser tuberosity.

(iii) The length measured to a point marking

the maximum lateral convexity of the greater tuberosity.

The estimated humerus length ranges between 188mm and 195mm and the means of the three ratios range between 190mm and 193mm. LeGros Clark and Leakey conclude that the total length of the bone most likely did not exceed 193mm. Because the humerus is so complete, exclusive use of the three brachiating genera as the reference sample most likely has not distorted the length measurement and this figure can be accepted as a reasonable estimate of the total length of the fossil. LeGros Clark and Leakey do not state whether their estimated length is the head capitulum length or the head/trochlear length. In the case of Dendropithecus this is not a problem, however. The trochlea does not project distally beyond the level of the capitulum.

(b) Humerus circumference - the midshaft diameters and circumference are given in Table III. 3. The circumference was computed by the author from the following formula given in LeGros Clark and Leakey (1951) ·

$$\frac{\text{Humerus Circumference X 100}}{193} = 19.3$$

(c) Radius length - the right radius fragment is composed of the proximal joint and proximal part of the shaft. This existing fragment measures 125mm in length. LeGros Clark and Leakey estimate the total length to be between 184 - 213mm, and suggest it is unlikely that the length of the radius exceeded the mean value of 200mm. The estimate is based on the ratio of the following two measure-meants to the total length of the bone. The

comparative sample was six specimens representing the genera Hylobates and Symphalangus.

(i) Length from the tip of the styloid process to the point of maximum lateral convexity.

(ii) The distance between the most proximal point of the head of the radius and the proximal extremity of the tuberosity.

This estimate must be considered more unreliable than the estimate of the humerus length. This is due to the more fragmentary nature of the bone and the exclusive use of the two genera of extant primate with the most elongated radii.

(2) Hindlimb

(a) Femora - the femur is represented by four incomplete shafts which have been labelled specimens I - IV. Because of its small size specimen IV is thought to be a juvenile.

Specimen I - This specimen is the most complete and is the shaft of a right femur from the lesser trochanter to the upper part of the popliteal surface. The lower portion of the shaft is detached and separated from the main fragment by an estimated 2 - 3 mm.

Specimens II and III - These specimens are both distal portions of the shafts of two right femura.

The total length of the femur was reconstructed on the basis of Specimens I and III which correspond roughly in size. The combination of these specimens allows an estimate of the length of the femur between the midpoint of the summit of the lesser trochanter and the medial condyle. The total length was determined as the ratio of this measurement to

total bone length using fourteen specimens representing modern gibbons, cercopithecines and atelines, as a comparative sample. The estimated total length is 214mm (205 - 226mm). It is not clear if this is the functional femoral length or the length from the greater trochanter to the medial condyle.

(a) Femur Midshaft measurements - the midshaft measurement from LeGros Clark and Leakey (1951) are given in Table III. 3.

(b) Tibia length - the tibia is represented by the major portion of the shaft of a right tibia which lacks the head and distal end. The fragment measures 163mm. LeGros Clark and Leakey estimate a total length between 190 - 200mm. This specimen is larger than juvenile femur (Specimen IV), however, it is not clear to which of the adult specimens it belongs.

III. 3. (1) Oreopithecus bambolii

The post cranial bones of Oreopithecus bambolii are known only from the articulated skeleton recovered in 1959 by J. Hurzeler from a coal mine near Grosseto in Tuscany, Italy. Based on the dentition the skeleton is male and fully adult. According to recent dating, the deposits are Late Miocene, approximately 9 million years (Andrews, pers. comm). Although a complete description has not been published, Schultz (1960) published a brief description of the post crania from which the measurements in Table III. 3 are taken. These measurements must be considered to be provisional, however. The skeleton was distorted during fossilisation and inspection of the photographs and casts shows that the two humeri are of considerably different lengths. In addition, a footnote, Schultz (1960) reports than an X-ray of the left femur shows a fracture just distal to the well preserved lesser trochanter

and, more important, that the proximal part of the bone had been pushed approximately 18mm over the distal portion. This would increase the femur length reported by Schultz (243mm) by 18mm and give a total length of 261mm. Therefore, until the entire skeleton can be examined in detail the accuracy of the reported measurements must be considered merely tentative.

In addition, the femur circumference reported by Schultz (79mm) must be considered extremely suspect. This figure was not achieved through direct measurement, but by applying the formula for the circumference of a circle to the measured transverse diameter of 25mm. This, most likely, greatly overestimates the true circumference. The femur has suffered anterior-posterior distortion, which has most likely altered the transverse diameter and, in addition, the shape of the cross section of the femora of a large bodied non-human primate tends to be elliptical with a sagittal diameter considerably smaller than the transverse diameter, thus decreasing the circumference even if the transverse diameter were correct. Section VII also shows that this measurement is grossly inconsistent in comparison with any other known higher primate, fossil or recent.

111 3. (j) KNM-ER-1503 / 1504

KNM-ER-1503 is a proximal femur and KNM-ER-1504 a distal humerus. These bones have been referred to Australopithecus sp. (Leakey, 1973c, Day, 1976). There is no certainty that they belong to the same individual, although both were found at the same site and at the same level (Koobi Fora, Area 123 from the level of, or slightly above, the KBS tuff). The proximal femur (1503) was found in 1972 by M. Muluila and the distal humerus (1504) by M. Mbithio. Other post cranial material found at the same site and level which are also assigned to Australopithec are ·

1. 1505 - the head and neck of a left femur and part of the distal shaft.
2. 1686 - parietal fragments
3. 1822 - femur shaft.

McHenry (1978) predicts the length of the humerus by a multiple regression formula based on the biepicondylar width and the distance between the trochlea and the medial epicondyle. Using Homo sapiens as a reference sample the length is 296.1mm and using Pan troglodytes as a reference the distance is 296.9mm. The consistency between these two predictions and inspection of the cast of the bone suggests that a length in this region is a reasonable estimate. This length is the head to trochlear length and, therefore, is consistent with the length measurement in this analysis (Section III.5).

To predict the length of the femur, McHenryuses a regression formula based on the distance from the most proximal point on the head to the distal border of the lesser trochanter measured parallel to the shaft and the total neck length (projected distance between the most lateral point on the greater trochanter to the most medial point on the head of the femur measured perpendicular to the shaft). Based on the modern Homo sapiens sample the length is 389.8mm and on the Pan sample the length is 330.6mm. The large difference between these estimates reflects the relatively long shaft in Homo sapiens and the relatively short shaft in Pan, and would suggest that the measurements used by McHenry are not good predictors for femur length across species. And, further, there is no certainty that these measurements stand in the same relationship to femur length in Australopithecus as they do in either Homo or Pan, given the unique morphology of the neck region of the femur in Australopithecus. In addition, confidence limits are not given for these predictions. However, a multiple correlation coefficient

of .88 for both the humerus and femur prediction based on the Homo sapiens sample, would suggest fairly wide confidence limits. In fact, based on these formulae, reported standard deviations for humerus length are in the range of 23mm and for femur length, 30mm. Therefore, little confidence can be placed on the femur length predictions. However, the maximum femur lengths for KNM-ER-1503, predicted on the basis of the Homo sapiens sample is of interest in relation to the relatively secure humerus length estimate, and will be discussed in Chapter IX.

III. 3. (k) Australopithecus reconstruction - Walker (1973)

In 1973 Walker published a composite reconstruction of an Australopithecus femur. This reconstruction was based on two East African specimens.

1. KNM-ER-993 - the distal three quarters of a right femur with a proximal fracture just below the lesser trochanter. This specimen was found in 1971 at Ileret between the upper and middle tuffs.
2. OH-20 - the proximal portion of the left femur lacking the head, part of the greater trochanter and lesser trochanter. It was found in 1959 at Olduvai Gorge, Tanzania. It is from the site HWK at the interface between Bed I and lower Bed II.

The bicondylar length of the reconstruction is estimated to be 360mm, and the robusticity index ($\frac{\text{average diameter}}{\text{length}} \times 100$) is given as 15.36. This gives an average diameter of 55.3mm.

III. 3. (l) KNM-ER-739

KNM-ER-739 is an almost complete right humerus which is missing only the head and a small portion of the proximal end of the shaft. It has been referred to the genus Australopithecus (Leakey, 1972). It was found in

1970 at Area 1, Ileret, and dates to approximately 1.3 m.y. (Maglio, 1972). The bone is very robust and has strong muscle impressions. The total length of the fragment is 310mm from the capitulum to the fracture. McHenry (1974) has predicted the total length of the humerus based on a multiple regression equation using the length from the trochlear to the lesser trochanter and the length to the greater trochanter. This produces a total length of 327.9 ± 6.8mm. Although the reference sample was modern Homo sapiens, this estimate is reasonable when compared to the cast.

111 3. (m) KNM-ER-1481

KNM-ER-1481 is an associated set of left lower limb bones including a virtually complete femur (1481a), the proximal end of the tibia (1481b), the distal end of the same tibia (1481c) and the distal portion of the fibula. The material has been assigned to the genus Homo (Leakey, 1973a, 1973b, Day et. al., 1975). It was found in 1972 at area 131 (Ileret) in the Koobi Flora formation and lies below the KBS tuff. Measurements of the femur given in Table III.3 are taken from Day et. al. (1975). These authors note that the shaft was broken into four pieces, but that the pieces fit together well, and the length measurement is accurate. There is some flaking and abrasion on the shaft, however, which may have slightly reduced the sagittal and the transverse diameters.

There has been no attempt in the literature to reconstruct the total length of the tibia. The published measurements for the fragments are given in Day et. al. (1975). The distal fibula fragment measures only 36mm from the distal and proximally to the fracture, and therefore, gives no information relevant to the total length of the tibia.

111. 3. (n) AL-288-1, Hadar, Ethiopia

The Hadar skeleton is the most complete

associated skeleton from the Plio-Pleistocene time period. An estimated 40% of the skeleton is present, including a complete left femur and a complete, although slightly crushed, right humerus. Although the skeleton was found in 1974, length measurements have only been published for these two bones and there are no midshaft measurements available. The length of the femur is 280 mm and the length of the humerus is approximately 235 mm (Johanson and Taieb 1976).

The skeleton was found in November 1974 near the bottom of the upper, or Kada Hadar, member at an approximate distance of 30 - 40 meters above the basalt layer in the upper portion of the Sidi Haxoma Member, which has yielded a potassium-argon date of 3.0 million years. The entire formation corresponds to the Usno formation and the Basal Member and Members A and B of the Shung ra formation in the Omo River sequence, which have been dated to approximately 2.6 - 3.1 million years (Taieb et al., 1976). The skeleton most likely approaches the 2.6 million year date. Morphologically there are certain similarities in the pelvis to the Sterkfontein 14 Australopithecus africanus skeleton, however, differences in the acetabulum, illium and mandibular dentition have suggested that this skeleton retains more primitive features than Sts 14 (Taieb et al., 1976). Recently Johanson and White (1979) have suggested that this skeleton, along with the rest of the hominid fossil material from Hadar, as well as the hominid fossil material from Laetoli, Tanzania, belongs to only one species which they have named Australopithecus afarensis.

111. 3. (o) Mesopithecus pentelici

Mesopithecus pentelici is a colobine monkey of small to medium size. It is known from the Late Miocene of Eurasia. The largest collection of

Mesopithecus fossils have been collected from Pikermi, Greece, since the 1830's.

Szalay and Delson (1979) describe the post cranial skeleton as combining distinctly colobine morphological features with other features suggesting a more terrestrial locomotor pattern than observed in any extant colobine. Among those features suggesting a terrestrial locomotor pattern are details of the elbow joint and the robusticity of the phalanges. In addition, the robusticity of the long bones is greater than that in modern colobines and most similar to the larger macaques. Szalay and Delson conclude that Mesopithecus was a colobine that had begun to converge on a more terrestrial way of life similar to modern macaques and was probably at least as terrestrial as the most terrestrial living colobine, Presbytis entellus.

Post cranial measurements employed in the allometric analyses (Table III. 3) are based on a female skeleton reconstructed from unassociated bones (Gaudry, 1862). The measurements are taken from Zapfe (1960).

111. 4. Body Weight Sample

Body weight data has been collected for a total of 80 species of extant higher primates. Appendix II provides the mean body weights and sample sizes for the males and females of each of these higher primate species. In the great majority of the cases, these weight data have been gathered from the literature and provided by Rudder (pers. comm., 1977). These data present wild weights wherever possible. However, the majority of the weight data does not come from the individual skeletons which were used as the source of the skeletal measurements. Because of the possible error this would introduce into the allometric analyses, species for which weight information is based on only one individual , or

species for which skeletal measurements come from only one individual, are not included in the allometric analyses involving body weight presented in Chapters V and VI. However, for comparative purposes, these species are included in the discussion of results in Chapter IX.

III. 5. The Skeletal Measurements

The skeletal measurements were taken on the vertebral column, the sacrum, the pelvis, the humerus, the radius, the femur and the tibia.

1. The Skeletal Trunk Length (Fig. III. 2)

The Skeletal Trunk Length, or Rumpskeletlänge, has been used by Biegert and Maurer (1972) and by Halazeck (1972) as a measure of body size in allometric analyses of the primate postcranial skeleton. The Skeletal Trunk Length is determined by the addition of the following measurements. These measurements were taken with Mitutoyo dial calipers accurate to .05 mm.

a) Vertebrae -- the maximum length of the ventral surface of the corpus of each thoracic and lumbar vertebrae.

b) Sacrum -- the length from the most ventral point on the sacral corpus perpendicular to the most anterior point of the auricular surface. This measurement was taken by placing a straight edge across the ventral surface of the sacral corpus and measuring with dial calipers perpendicularly to the most anterior point of the auricular surface.

c) Pelvis -- the distance from the most anterior point of the auricular surface to the most caudal point of the ischium in the axis of the ischium.

III. 5. 2. The Length of the Long Bones of the Appendicular Skeleton

Wherever possible, the bones of the left side of

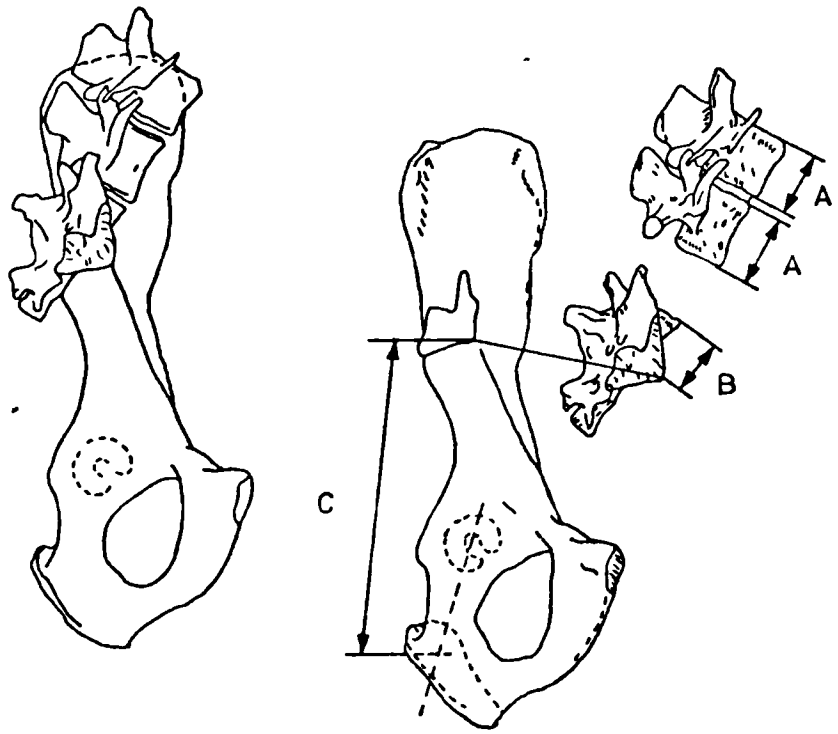

Fig. III. 2. The skeletal trunk length is a composite measurement made up of the sums of measurements 'A', 'B' and 'C'. Measurement 'A' is the maximum length of the ventral surface of the corpus of each thoracic and lumbar vertebrae. Measurement 'B' is the length from the most ventral point on the sacral corpus perpendicular to the most anterior point of the auricular surface. Measurement 'C' is the distance from the most anterior point of the auricular surface to the most caudal point of the ischium in the axis of the ischium.

the skeleton were measured. However, in isolated cases where the left bones were missing or damaged, the bones of the right side were measured. Bones exceeding 150 mm in length were measured on a standard osteometric board accurate to the closest millimetre. Shorter bones were measured with Mitutoyo dial calipers accurate to .05 mm.

a) The Length of the Humerus -- the length of the humerus is measured from the most proximal point of the head to the most distal point of the trochlea. The humerus is placed with its posterior surface down and the most lateral point of the great tuberosity and the external condyle parallel to the axis of measurement.

b) The Length of the Radius -- the length of the radius is taken from the most proximal point on the head to the most distal point on the styloid process. The radius is placed with its anterior surface down and the most medial point of the radial tubercle and the most medial point of the distal articular surface parallel to the axis of measurement.

c) The Length of the Femur -- the length of the femur is taken from the most proximal point on the head of the femur to the most distal point on the condylar articular surfaces. The femur is placed with its posterior surface down and the condylar articular surfaces on a plane perpendicular to the axis of measurement.

d) The Length of the Tibia -- the length of the tibia is taken from the most proximal point on the tibial spine to the most distal point on the talar articular surface. The tibia is placed with its

posterior surface down and the most medial point of the inner tuberosity and the internal malleolus parallel to the axis of measurement. A steel spacer of known length is placed between the most distal point on the talar articular surface and the vertical slide of the osteometric board. The length of the spacer is then subtracted from the total distance read from the osteometric board to give the desired length of the tibia.

111. 5. 3. The Circumference of the Femur and the Circumference of the Humerus

The circumference of the femur and of the humerus are taken at the midpoint of the shaft determined by the length measurements. A piece of dental floss is wrapped around the shaft and the point at which one circumference is made is marked on the floss with pencil. The circumference is then measured from the floss to the closest millimetre on a steel rule.

111. 6. Measurements taken on X-rays

Both the humerus and the femur of 221 skeletons were x-rayed in two planes, the sagittal and the transverse. These x-rays provide the source for the following measurements.

1. Bone Diameter -- the diameter of each long bone is measured in both the sagittal and the transverse planes. These measurements are taken perpendicular to the shaft of the bone at the midpoint.

2. The Diameter of the Medulla -- the diameter of the medulla of each long bone is measured in both the sagittal and the transverse planes. This measurement is taken perpendicular to the shaft of the bone at the midpoint.

III. 6. 3. The Average Cortical Thickness of the Midshaft of the Long Bone -- the average cortical thickness of the midshaft of the long bone is determined in the following way.

a) The transverse medulla diameter is subtracted from the transverse bone diameter.

b) The sagittal medulla diameter is subtracted from the sagittal bone diameter.

c) The results of both a) and b) are added together and divided by 4.

The midpoint of the shafts of both the femur and the humerus is determined on the basis of their length measurements (Section III. 5). This point is marked on the bone before x-ray exposure with a piece of split shot embedded in plasticine. The measurements are taken in a darkened room with all of the x-ray, except for the bone being measured, masked from view. The measurements are made with Mitutoyo dial calipers accurate to .05mm. A piece of clear plastic is placed over the x-ray during measurements to protect it from scratches.

The precise orientation of the bones at the time of exposure is essential to the consistency of the measurements taken from the x-rays. Each bone is orientated according to the following system, and held in place with plasticine during exposure. The shafts of the bones are in direct contact with the film holder during exposure.

1. The Humerus

a) Sagittal Orientation - the humerus is placed with its medial surface down. The most projecting points of the internal and external condyles are positioned vertically over one another by measuring an equal distance to each condyle from a vertically orientated bubble level.

b) Transverse Orientation - the humerus is placed with its posterior surface down. The most projecting points of the internal and external condyles are levelled by measuring an equal distance to each condyle from the horizontal surface of the film holder.

111. 6. 3. 2. The Femur

a) Sagittal Orientation - the femur is placed with its lateral surface down. The popliteal surface is vertically oriented by placing it against a surface at right angles to the horizontal film holder.

b) Transverse Orientation - the femur is placed with its anterior surface down. The popliteal surface is levelled with a bubble level.

111. 7. Measurement Error

Measurements for the allometric analyses are taken directly from the long bones as well as from x-rays of the long bones. Those measurements taken directly from the long bones are the bone lengths and the circumferences of the midshafts of the long bones. Those measurements taken from the x-rays are the sagittal and transverse diameters of the midshaft of the long bones and the sagittal and transverse diameters of the medulla of the long bones.

In the following analysis of measurement error a human humerus is used as the source for measurements of the transverse diameter of the midshaft measured both directly from the bone as well as from x-rays of the bone.

A. Measurement of the transverse diameter of the midshaft taken directly from the bone

1. Measurements -- Ninety measurements were taken on the transverse diameter of the midshaft of the humerus. These ninety measurements are composed of ten consecutive measurements taken at nine separate times.

2. Mean = 16.59 mm

3. Standard Deviation = .056

B. Measurements of the transverse diameter of the midshaft taken from x-rays

Two x-ray tube heights were used in taking x-rays of the bone cross sections, 100 cm and 175 cm. Measurement error is determined for exposures at both tube heights. Eighty measurements are taken on the same x-ray at each tube height. These eightly measurements are composed of ten consecutive measurements taken at eight separate times.

1. 100 cm tube height

Mean = 16.53 mm

Standard Deviation = .1089

2. 175 cm tube height

Mean = 16.49 mm

Standard Deviation = .1149

From the above it can be concluded that the mean of the measurements of the transverse diameter of the midshaft of the human humerus taken from the x-rays lie within two standard deviations of the mean of the transverse diameter measurements taken on the bone itself.

These x-ray exposures are taken with the bone in the centre of the film directly below the tube. The position of the bone on the film effects the magnitude of the measurements taken from the x-ray exposures. As the bone is moved laterally away from the centre of the film directly below the tube, the magnitude of the measurement increases.

The effect of this increase in magnitude is tested for both tube heights over a distance of eight inches from the centre of the film. Positions 1 through 4 indicate distance from the centre of the film, 1 being at the centre and 4 being eight inches from the centre. Ten measurements are taken on the x-ray exposure at each position.

1. 100 cm tube height

	1	2	3	4
Mean	16.60	16.79	16.97	17.18
S.D.	.0333	.0337	.0337	.0422

2. 175 cm tube height

	1	2	3	4
Mean	16.57	16.61	16.75	16.79
S.D.	.0333	.0337	.0337	.0422

In both of these comparisons, the magnitude of the measurements of the transverse diameter of the

midshaft of the humerus cross section increase as the bone is placed further away from the centre of the film. However, the increase is less at the higher tube height. Even at the lower height, however, the maximum deviation of the mean of the transverse diameter measurements (17.18 mm) is only 0.59 mm from the mean transverse diameter measurement taken on the bone itself.

Because of equipment constraints, a tube height of 100 cm is used for the x-ray exposures of the human bones taken at the Smithsonian Institution. A tube height of 175 cm is used for the non-human primate skeletons x-rayed at the British Museum (Natural History). In addition, in both cases bones are positioned as close as possible to the centre of the film directly below the tube.

The above results indicate that there is a reasonable correspondance between measurements made directly on the bone and measurements taken from x-ray exposures. In the worse case, at a tube height of 100 cm when the bone is positioned eight inches from the centre of the film, x-ray measurements are accurate to 3.5% of measurements taken directly on the bones. In the great majority of cases, where the tube is higher and the bone positioned closer to the centre of the film, the measurement error is considerably less.

111. 8. Computed Strength Measurements of the Cross Section of the Long Bones

Two strength measurements are calculated for the cross section of both the femur and the humerus. The section modulus represents the strength of the cross section of a long bone in bending. The area of the cross section of a long bone represents its strength in compression.

1. Section Modulus

The section modulus is a measure of the strength of the cross section of a column (or long bone) in bending. It is dependent on both the amount and the distribution of material in the cross section and, therefore, represents in one measure the size and the shape of the cross section as well as the cortical thickness. It is derived from the following formula (Lovejoy, et al., 1976).

$$Z = I/y$$

where Z = the section modulus

y = the distance from the neutral line to the edge of the cross section in the axis of bending

I = the area moment of inertia and is derived from the following

$$I = a_1 d_1^2$$

where a = the area of each small unit of the cross section designated for calculation

d = the perpendicular distance f rom the centre of each unit to the neutral axis in the plane of bending

The stress at any point on the cross section is determined by

$$s = My/I$$

where s = stress

M = bending moment which is composed of weight times the perpendicular distance from the centre of gravity of the weight to the neutral axis of the cross section

y = perpendicular distance from the neutral line to the point on the cross section for which the stress is to be determined in the plane of bending

I = the moment of inertia

In the above the stress increases with an increase of y if both M and I are held constant. Therefore, in any cross section the maximum stress is found at the edge of the section. This is represented in the following equation

$$s_{max} = My_{max}/I$$

This is equivalent to

$$s_{max} = \frac{M}{I/y_{max}}$$

and is also equivalent to

$$s_{max} = \frac{M}{Z}$$

The computation of the section modulus requires the sectioning of the bone, or the use of computed tomography (Jungers and Minns, 1979), to determine the amount and the distribution of cortical bone in the cross section. If, however, the cross section can be assumed to be a circle or an ellipse, the section modulus can be determined by the following formula

$$Z = \frac{n(A^3B - a^3b)}{32A}$$

where A = the external diameter of the cross section in the plane of bending

B = the external diameter of the cross section in the plane perpendicular to the direction of bending

a = the diameter of the medulla in the plane of bending

b = the diameter of the medulla in the plane perpendicular to the direction of bending

The section modulus is computed in this fashion for the femur and the humerus, the cross sections of both bones approximating the required geometrical shape. The diameters are taken from the x-rays and bending is assumed to be in the sagittal plane.

111. 8. 2. The Area of the Cross Section

The area of the cross section of a long bone refers to the actual area of the cross section that is composed of cortical bone. As with the computation of the section modulus, the actual area of the cross section of a long bone can only be determined by sectioning the bone or through the use of computed tomography. However, if the cross section can be assumed to be a circule or an ellipse, the area of the cross section can be determined by the following formula

$$\text{Area} = \frac{(A-a)(B-b)}{4}$$

where A = the sagittal diameter of the cross section

a = the sagittal diameter of the medulla

B = the transverse diameter of the cross section

b = the transverse diameter of the medulla

The area of the cross section is computed in this fashion for both the femur and the humerus. The diameters are measured from x-rays.

III. 9. Equipment List

I. Skeletal Meansurements

1. Mitutoyo dial calipers accurate to .05 mm.
2. Standard osteometric board
3. Dental floss - used to measure the circumference of the long bones.
4. Steel millimeter rule - used to measure the circumference of the long bone from the dental floss.

II. X-raying

1. X-ray machines
   a. Smithsonian Institution - Picker x-ray machine.
   b. British Museum (Natural History) - Phillips Industrial machine
2. Tube height
   a. Smithsonian Institution - 100 cm.
   b. British Museum (Natural History) - 175 cm.
3. Exposure
   a. Smithsonian Institution
      72 kV, 15 Ma, 10 sec.
      79 kV, 15 Ma, 10 sec.
   b. British Museum (Natural History) -
      60 kV, 15 Ma, 30 sec.
4. Kodak X-Omat L Film (number XL 5) was used throughout.

III. X-raying aids

1. Split shot - used to mark measuring points on the bone before x-raying.
2. Plasticine - used to secure split shot to bone and to aid in the positioning of the bone on the film.
3. Bubble level - used to aid in the positioning of the bone before x-raying.
4. Square wooden block - used to vertically align bones for x-raying.

IV. Measuring from the x-rays

1. Mitutoyo dial calipers accurate to .05 mm.
2. Light box
3. Black paper to mask all of the x-ray exposure except that part being measured.
4. Millimeter steel rule
5. Plastic sheet - used to protect the x-ray exposure from scratches during measurement.

V. Calculation of statistics

1. HP97 -- Helwitt Packard programmable calculator.
2. Programs - written by the author.

111. 10. Allometric Statistics

The allometric equation is generally presented in the following form (Huxley, 1932, Gould, 1966).

$$\log Y = \log A + b \log X \qquad \text{Eq. 1}$$

This is the equation for a sloping straight line where (1) logX and logY are the logarithmic transformations of the two variables, X and Y, (2) log A is the point at which the sloping line will intercept the Y axis when X is zero, and (3) b is the slope of the line. The logarithmic transformation is normally used in allometric analyses to transform a curvilinear relationship into a linear relationship for simplicity of curve fitting. Equation 1 represents the following exponential relationship:

$$Y = AX^b$$

There is an additional reason for employing the logarithmic transformation which is often overlooked in allometric analysis. The logarithmic transformation tends to equalize variances over large size ranges as well as provide a reasonable approximation to a normal distribution (Sokal and Rohlf, 1969). Because equal variance and normal distributions are basic assumptions of most of the techniques of curve fitting, it is imperative to carry out allometric analyses on logarithmically transformed data.

There are a number of techniques of fitting a straight line to bivariate data. The correct choice of technique depends on the purpose of the investigator in fitting the line. In most allometric analyses there are three purposes. Firstly, is the characterisation of the trend of the relationship between the two variables. This involves the determination of the allometry or isometry of the relationship. Secondly is the comparison of two or more populations. And, thirdly, is the prediction of Y values based on the analysis. In much of the literature on allometry least squares regression analysis has been employed to satisfy all three of these purposes. This is invalid. Although least squares regression is a suitable technique for the comparison of populations and for prediction, it does not always give an accurate characterisation of the trend of the relationship between the two variables. Least squares regression is designed for experimental situations where one variable, the independent variable, is fixed by the

investigator and is, therefore, sampled without error, while the second variable, the dependent variable, is sampled from the population of possible dependent variables for each independent variable. The least squares regression line is that line which minimises the squared deviations from the observations (the values of the dependent variable) to the line measured parallel to the Y axis. Therefore, in data such as that often encountered in allometric analyses where neither variable is independent, two different regression lines can be fitted to the data depending on which variable is considered to be independent for the sake of the analysis. As the equations in the next section show, the lower the correlation coefficient of these two variables the more these two lines will differ. Therefore, neither line will accurately characterise the trend of the bivariate relationship unless the correlation coefficient is very high. If the purpose of the analysis is to establish the allometry or isometry of a specific relationship techniques which provide one line which characterise the trend of the bivariate relationship are more appropriate. These will be discussed in Section III.10.4

III. 10 (a) Least Squares Regression Analysis

If the data meet the following assumptions, least squares regression analysis can be employed for purposes of prediction of population comparison.

Assumptions for least squares analysis (Snedecor and Cochran, 1956).

a) For every X the Y's are assumed to be independently and normally distributed.

b) The Y's for each X have a common variance.

c) The expected value, Y, for any given X is described by a linear function.

Assumptions a) and b) can often better be met by the logarithmic transformation of the data. The logarithmic transformation will be used throughout this analyses. If there is reason to believe that assumption c) is not fulfilled by the data a test for linearity can be applied. (Snedecor and Cochran, 1956).

Least square regression equations (Rohlf and Sokal, 1969).

111. 10. (a) 1. Introduction

The basic least squares equation is ·

$$Y = a_{y\cdot x} + b_{y\cdot x}X \qquad \text{Eq. 1}$$

where X = logX, the logarithm of the independent variable

Y = logY, the logarithm of the dependent variable

$a_{y\cdot x} = \bar{Y} - b_{y\cdot x}\bar{X}$

$b_{y\cdot x} = \Sigma xy / \Sigma x^2$

Σxy = the sum of products of the two variables

Σx^2 = the sum of squares of X

If X is the dependent variable and Y the independent variable the equations become ·

$$X = a_{x\cdot y} + b_{x\cdot y}Y$$

where $a_{x\cdot y} = \bar{X} - b_{x\cdot y}\bar{Y}$

$b_{x\cdot y} = \Sigma xy / \Sigma y^2$

Σy^2 = the sum of squares of Y

the slope of $b_{x\cdot y}$ is related to the slope of $b_{y\cdot x}$ through the correlation coefficient (r_{xy}) in the following manner

$$r_{xy} = \frac{\Sigma xy}{\sqrt{\Sigma x^2 \Sigma y^2}}$$

$$= \frac{\Sigma xy}{\sqrt{\Sigma x^2}} \cdot \frac{1}{\sqrt{\Sigma y^2}}$$

multiplying the numerator and denominator by $\sqrt{\Sigma x^2}$

$$r_{xy} = \frac{\Sigma xy}{\sqrt{\Sigma x^2}\sqrt{\Sigma x^2}} \cdot \frac{\sqrt{\Sigma x^2}}{\sqrt{\Sigma y^2}}$$

$$r_{xy} = \frac{\Sigma xy}{\Sigma x^2} \cdot \frac{\sqrt{\Sigma x^2}}{\sqrt{\Sigma y^2}}$$

Dividing numerator and denominator by $\sqrt{N-1}$

$$r_{xy} = \frac{\Sigma xy}{\Sigma y^2} \cdot \frac{\sqrt{\frac{\Sigma x^2}{N-1}}}{\sqrt{\frac{\Sigma y^2}{N-1}}}$$

And from Eq. 1 ·

$$r_{xy} = b_{y \cdot x}\left(s_x / s_y\right)$$

where $s_x = \sqrt{\frac{x^2}{N-1}}$ = standard deviation of X

$s_y = \sqrt{\frac{y^2}{N-1}}$ = standard deviation of Y

And therefore

$$b_{y \cdot x} = r_{xy}\left(s_y / s_x\right) \qquad \text{Eq. 2}$$

In a similar fashion the following relationships can be proven to be true ·

$$r_{xy} = b_{x \cdot y}\left(s_y / s_x\right)$$

and

$$b_{x \cdot y} = r_{xy}\left(s_x / s_y\right) \qquad \text{Eq. 3}$$

From Eq. 2 and 3

$$(b_{x \cdot y})(b_{y \cdot x}) = r_{xy}\, s_x / s_y\, r_{xy}\, s_y / s_x = r_{xy}^2 .$$

Therefore

$$r_{xy} = \sqrt{(b_{y \cdot x})(b_{x \cdot y})}$$

And ·

$$b_{x \cdot y} = r_{xy}^2 \Big/ b_{y \cdot x}$$

And ·

$$b_{y \cdot x} = r_{xy}^2 \Big/ b_{x \cdot y}$$

To summarise, the amount by which the slopes $b_{x \cdot y}$ and $b_{y \cdot x}$ vary from a reciprocal relationship, or identity, is proportional to the square of the correlation coefficient.

111. 10. (b) Uses of Least Squares Regression Analysis - Comparison of Populations

Two bivariate populations can be distinguished by one or both of the following criteria. Firstly, they can be distinguished by a significant difference in the slopes of the two populations, and secondly by a significant difference in the Y intercepts of the two populations.

The slopes and Y intercepts of samples may be tested in order to determine whether they were drawn

from populations with distinct slopes and/or Y intercepts. Confidence limits may be computed for both the sample slopes and Y intercepts. If the confidence limits for the slopes of the two samples overlap those two samples cannot be assumed at that level of confidence to have been drawn from populations with different slopes. The same type of test can be performed for the Y intercepts.

111. 10. (b) 1. Confidence limits for $B_{x \cdot y}$ (Sokal and Rohlf, 1969).

$$b_{x \cdot y} \pm t_{(.05)} \frac{S^2_{x \cdot y}}{y^2}$$

where $S^2_{x \cdot y}$ is the part of the variance of X that is not accounted for by its relationship with Y. This is often called the unexplained variance of X. It can be found by any one of the following three equivalent formulae

$$S^2_{x \cdot y} = \left(\Sigma x^2 - \frac{(\Sigma xy)^2}{\Sigma y^2} \right) \left({}^{1}/_{N-2} \right) \qquad \text{Eq. 1}$$

$$S^2_{x \cdot y} = (1 - r^2_{xy}) (S^2_x) ({}^{N-1}/_{N-2})$$

$$S^2_{x \cdot y} = \left[S^2_x - (b_{x \cdot y})^2 S^2_y \right] ({}^{N-1}/_{N-2})$$

$t_{(.05)(n-2df)}$ is read from the T-Table with N-2 degrees of freedom.

111. 10 (b) 2. Confidence limits for $b_{y \cdot x}$ are ·

$$b_{y \cdot x} \pm t_{(.05)} \frac{S^2_{y \cdot x}}{\Sigma x^2}$$

where · $S^2_{y \, x} = (\Sigma y^2 - \frac{(\Sigma xy)^2}{\Sigma x^2}) ({}^{1}/_{N-2})$ Eq. 2

$$S^2_{y \cdot x} = (1 - r^2_{xy}) (S^2_y) ({}^{N-1}/_{N-2})$$

$$S^2_{y \cdot x} = \left[S^2_y - (b_{y \cdot x})^2 S^2_x \right] ({}^{N-1}/_{N-2})$$

111. 10. (b) 3. Confidence limits for the Y intercept (Simpson et. al., 1960) are ·

$$a_{y \cdot x} \pm t_{a(N-2)} S_{y \, x} \sqrt{\frac{1}{N} + \frac{\bar{x}^2}{(N-1)(s^2_x)}} \qquad \text{Eq. 3}$$

where · $S_{y \cdot x} = \sqrt{S^2_{y \cdot x}}$ from Eq. 2 and

is the unexplained standard deviation of Y

$\bar{X}$ = the mean of the X's

$t_{a(n-2)}$ = t from the t-table with 'a' levels of significance and N-2 degrees of freedom.

4. Confidence limits for the Y intercept

$$a_{x\cdot y} \pm t_{a(N-2)} S_{x\cdot y} \sqrt{\frac{1}{N} + \frac{\bar{Y}^2}{(N-1)(S_y^2)}}$$

where $S_{x\cdot y} = \sqrt{S^2_{x\cdot y}}$ from Eq. 1

111. 10. (c) Uses of Least Squares Regression Analysis - Prediction

There are two types of prediction which are based based on the least squares relationship.

1. The prediction of μ (the population mean of Y's for a given X). This type of prediction does not involve the introduction of new individuals into the analysis. The determination of confidence limits for the Y intercept (Eq. 3, Section 111, 10.2) is a special case of this type of prediction where X = O.

2. Prediction of Y for a new individual of known X. This type of prediction involves the introduction of a new individual into the analysis and the estimation of Y for a known X for this individual based on the previous analysis.

Both Case 1 and Case II prediction involve the estimate of a Y for a given X, and differ only in the manner in which the confidence limits are set for the predicted Y.

1. Prediction of Y from a known X (from Eq. 1, Section 111.10.1)

$$\hat{Y} = a_{y\cdot x} + b_{y\cdot x} X$$

2. Confidence limits for Case 1 prediction ·

$$\hat{Y} \quad t_{a(N-2)} S_{y\cdot x} \sqrt{\frac{1}{N} + \frac{(X-\bar{X})^2}{\Sigma x^2}}$$

where X = the value of X for which the mean of the population of Y's is to be predicted. Other terms are as in Eq. 3, Section 111.10.2.

3. Confidence limits for Case II prediction ·

$$\hat{Y} \pm t_{a(N-2)} S_{y \cdot x} \sqrt{1 + \frac{1}{N} + \frac{(X-\bar{X})^2}{\Sigma x^2}}$$

4. Prediction of X from a known Y·

$$\hat{X} = A_{x \cdot y} + b_{x \cdot y} Y$$

5. Confidence limits for Case I prediction

$$\hat{X} \pm t_{a(N-2)} S_{x \cdot y} \sqrt{\frac{1}{N} + \frac{(Y-\bar{Y})^2}{\Sigma y^2}}$$

where Y = the value of Y for which the mean of the population of X's is to be predicted. Other terms are as in Eq. 3, Section III.10.2.

6. Confidence limits for Case II prediction ·

$$\hat{X} \pm t_{a(N-2)} s_{x \cdot y} \sqrt{1 + \frac{1}{N} + \frac{(Y - \bar{Y})^2}{\Sigma y^2}}$$

Fig. III3illustrates the confidence belts for the two cases of prediction. The confidence belt in Case II prediction is wider than that in Case I prediction because, in entering a new individual into the analysis, an additional random error for that individual must be considered (Snedecor and Cochran, 1956).

III. 10. (d) Determining the Trend of the Bivariate Relationship

There are two major techniques for determining the trend of a bivariate relationship, major axis or principal axis (Sokal and Rohlf, 1969) and reduced major axis (Teissier, 1948; Kermack and Haldane, 1950, Gould, 1966). Principal axis analysis provides an unbiased estimate of the long axis of the ellipse which circumscribes the bivariate normal population from which the sample is drawn. It corresponds to the first principal component in multivariate analysis and has the advantage of being computed from simple statistics (X, Y, s_x^2, s_y^2, sxy). The only assumption is a bivariate normal distribution. The one disadvantage of principal axis analysis is that the slope is dependent on the scale of

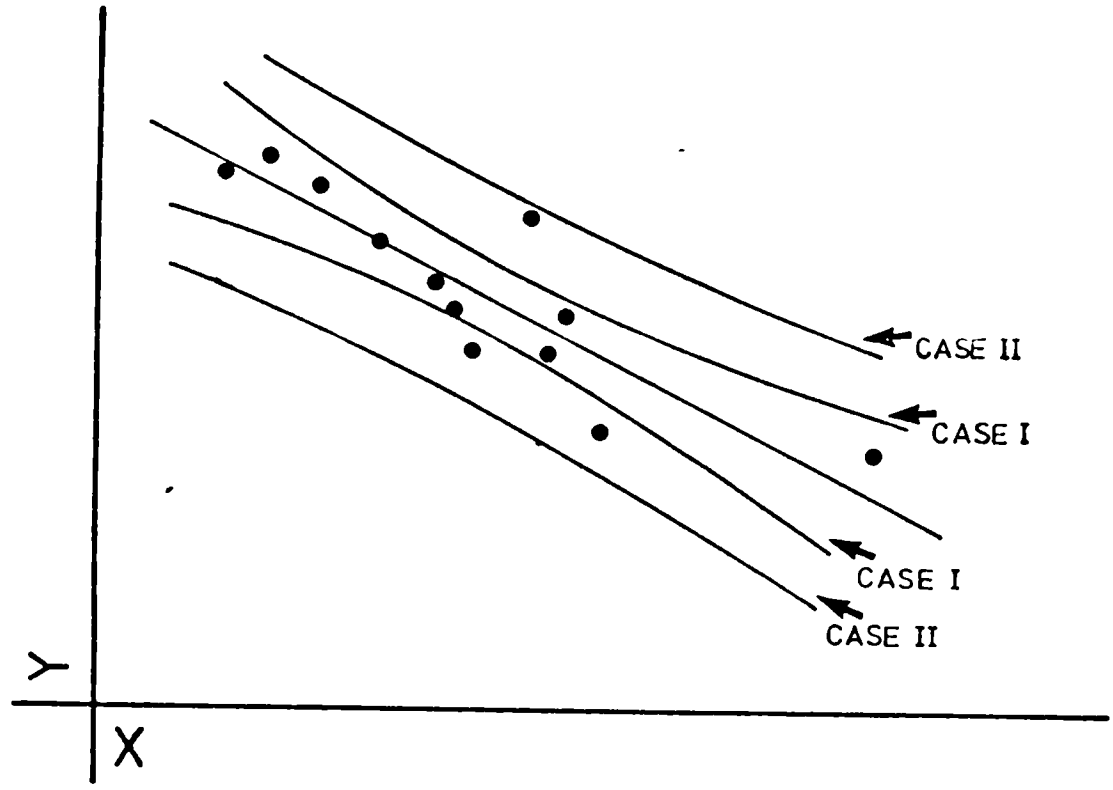

Fig. III. 3. Confidence limits for least squares Case '1' and Case '2' predictions of an unknown 'Y' from a known 'X'.

measurement (Teissier, 1948; Kermack and Haldane, 1950). Therefore, slopes in two analyses using two different scales of measurement could not be readily compared. If a logarithmic transformation is employed the scale is invariant and this criticism disappears. However, at the time when the second technique, reduced major axis analysis, was suggested as a possible scale invariate alternative, the lack of computers made logarithmic transformations cumbersome. The reduced major axis is simply the major axis of the variables standardised to a variance of 1. It has the advantage of being easier to compute than the major axis, involving only the sums and the sums of squares of the two variables, and also of being a more efficient estimator of the slope under certain conditions (See Kermack and Haldane, 1950, for further discussion). In practice, however, both principal axis and the reduced major axis analyses give similar results on logarithmically transformed data. With both of these techniques, however, it is possible to fit lines to an array of almost randomly scattered points. The significance of the trend is largely dependent on the degree to which the variables covary. The product moment correlation coefficient provides a measure of the covariation and should be reported along with the principal axis or reduced major axis.

111. 10. (e) Equations for the Determination of the Principal Axis

1. The equation for the principal axis is:

$$Y = \bar{Y} + b_1(X - \bar{X})$$

where: $\bar{Y}$ and $\bar{X}$ are the means of the two variables X and Y

b_1 = the slope of the line

$= s_{xy}(\lambda_1 - s_y^2)$

$s_{xy} = \Sigma xy/N-1$ = the covariance of X and Y

$s_y^2 = \Sigma y^2/N-1$ = the variance of Y

$$\lambda_1 = \tfrac{1}{2}\left[s_x^2 + s_y^2 + \sqrt{(s_x^2 + s_y^2)^2 - 4(s_x^2 s_y^2 - s_{xy}^2)}\right]$$

This is the eigenvector or latent root for this relationship and is a measure of variability along the major axis.

The equation for the minor axis (b_2) which is perpendicular to the major axis is ·

$$b_2 = -1/b_1$$

The equation for the latent root corresponding to the minor axis is ·

$$\lambda_2 = \tfrac{1}{2}\left[S^2 + S_y^2 - \sqrt{(S_x^2 + S_y^2)^2 - 4(S_x^2 S_y^2 - S_{xy}^2)}\right]$$

2. The confidence limits for the slope are determined in the following fashion

$$H = \frac{X^2_{a(1)}}{(\lambda_1/\lambda_2 + \lambda_2/\lambda_1 - 2)N}$$

where $X^2_{a(1)}$ is the Chi-square score for the 'a' level of significance.

$$A = \sqrt{H/1 - H}$$

the lower limit for b_1 $= \dfrac{b_1 - A}{1 + Ab_1}$

the upper limit for b_1 $= \dfrac{b_1 + A}{1 - Ab_1}$

111 10. (f) Equations for the Determination of the reduced Major Axis (Kermack and Haldane, 1950).

1. The equation for the reduced major axis is ·

$$Y = \frac{s_y}{s_x} X + (\bar{Y} - \frac{s_y}{s_x} \bar{X})$$

where · $s_y/s_x = b$ = the slope

$\bar{Y} - s_y/s_x \bar{X}$ = the Y intercept

2. The standard error of the slope, b, is ·

$$S_b = s_y/s_x \sqrt{\frac{1-r^2}{N}}$$

3. The standard error of the Y intercept, $\bar{Y} - s_y/s_x \bar{X}$ is ·

$$S_a = \bar{Y} - \bar{X} S_b \pm s_y \sqrt{\frac{1-r^2}{N}(2 + X^2 \frac{2(1+r)}{S_x^2}}$$

111. 10. (g) The Product Moment Correlation Coefficient

The equation for the product moment correlation

coefficient is

$$r_{xy} = \frac{\Sigma xy}{(N-1)S_x S_y}$$

where Σxy = the sum of products of the two variables

S_x = the standard deviation of X

S_y = the standard deviation of Y

The square of the product moment correlation coefficient is called the coefficient of determination and gives the proportion of variance of one variable which is explained by the relationship of that variable with the second variable. This follows from ·

$$r^2_{xy} = \frac{(\Sigma xy)^2}{\Sigma x^2 \Sigma y^2}$$

$$= \frac{(\Sigma xy)^2}{\Sigma x^2} \cdot \frac{1}{\Sigma y^2}$$

The left hand term is the regression formula for the explained sum of squares of variable y on variable x. If the explained sum of squares of variable y on variable x is ·

$$\Sigma \hat{y}^2 = \frac{(\Sigma xy)^2}{\Sigma x}$$

then $$r^2_{xy} = \frac{\Sigma \hat{y}^2}{\Sigma y^2}$$

This is also true when variable x is regressed on variable y:

$$r^2 = \frac{(\Sigma xy)^2}{\Sigma x^2 \Sigma y^2}$$

$$= \frac{(\Sigma xy)^2}{\Sigma y^2} \cdot \frac{1}{\Sigma x^2}$$

Because ·

$$\Sigma \hat{x}^2 = \frac{(\Sigma xy)^2}{\Sigma y^2}$$

$$r^2_{xy} = \frac{\Sigma \hat{x}^2}{\Sigma x}$$

In addition, $1-r^2$ gives the ratio of the unexplained sum of squares to the total sum of squares. This is called the coefficient of nondetermination and is simply the proportion of the variance of a variable which is left unexplained by its relationship to a second variable.

III. 10. H. Significance Testing of Variances

The statistical test to determine whether or not the variances of two populations are equal is an F test. F in this case is the ratio of the greater variance (s_1^2) over the lesser one (s_2^2).

$$F = \frac{s_1^2}{s_2^2}$$

The critical F value for the test is $F_{a/2(v_1 v_2)}$ where 'a' is the level of error accepted and $v_1 = N_1 - 1$ and $v_2 = N_2 - 1$, the degrees of freedom, respectively. N_1 and N_2 are the sizes of each sample.

In the allometric analyses this test is used to determine the equality, or the inequality, of the variances left unexplained by pairs of allometric relationships.

III. 11. Samples used in the allometric analyses

Males and females of each primate species are included separately in the allometric analyses. In chapters IV, V, and VI only the Branch Sitting and Walking primates, the Old World Semibrachiating primates, Papio anubis as the sole representative of the Ground Standing and Walking primates, the apes and human beings are included in the statistical analyses of the allometric plots. The reason for this is the small sample sizes for the remaining primates (the New World Semibrachiating primates, the Part Ground Standing and Walking and Part Branch Sitting and Walking primates, and the remaining Ground Standing and Walking primates). Although these primates are not included in the statistical analyses, they are plotted for reference in the bivariate diagrams in these chapters.

In the statistical analyses in chapters IV through VI the primate sample is divided into two groups based on body size. Group 1, the smaller body-size group, includes

species of Colobus, Presbytis, Cercopithecus and Cercocebus (the Branch Sitting and Walking primates and the Old World Semibrachiating primates). Group 2, the larger body-size group, includes Papio, Pan, Pongo, Gorilla, and Homo. Allometric statistics are computed separately for these two groups as well as for the combined sample.

In chapter VII the primates represented by small sample sizes (the New World Semibrachiating primates, the Part Ground Standing and Walking and Part Branch Sitting and Walking primates and the remaining Ground Standing and Walking primates) as well as the fossil primates are discussed in relation to the allometric patterns presented in the earlier chapters. In chapter VIII (The Prediction of the Body Weight of Fossil Primates) all primates for which there are data, in spite of sample size, are included in the statistical analysis.

Table III. 1. gives the sample sizes for each sex of each species used in the analyses. Table III. 2. gives the species employed in the various analyses as well as the symbols used to represent the various locomotor groups in the bivariate plots. Other symbols used in the bivariate plots are the following

A	= Ateles	B	= Brachyteles
P	= Pan	Po	= Pongo
G	= Gorilla	Al	= Alouatta
L	= Lagothrix	H	= Hylobates

Maboko = Proconsul sp. indent.
Dendropithecus = Dendropithecus macinnesi
Pliopithecus = Pliopithecus vindobonensis
Mesopithecus = Mesopithecus pentelici
Oreopithecus = Oreopithecus bambolii
Paidopithex = Paidopithex rehanenus
P. africanus = Proconsul africanus
A. weinfurteri = Austriacopithecus weinfurteri
D. fontani = Dryopithecus fontani

IV. Measurements of Body Size and of the Midshaft Cross Section of the Long Bones

IV. 1. Introduction

It is clear from the foregoing literature reviews that published analyses of limb proportions and robusticity indices are highly ambiguous and, as a result, have had only limited interpretive significance. One of the reasons for this ambiguity is the failure to establish the significance of the measurements before they are included in either the computation of indices or in allometric analyses. This is particularly true of measurements which have been used as reference measurements to represent the body size of the animal, as well as of measurements which have been used with the specific purpose of representing the strength of the cross-section of a long bone.

In this chapter, the following relationships are tested

1. The significance of the skeletal trunk length as a measurement of body weight in the higher primates.
2. The significance of the external measurements of the cross-section of the long bones as measurements of the strength of the bone in compression and bending.

IV. 2. Skeletal Trunk Length as a Measurement of Body Size In the Higher Primates

Body weight is generally preferred as a measurement of body size in allometric analyses (Gould, 1966, 1975). However, as the result of the difficulty in finding skeletons for which known live body weights are available, its use has been limited in the analyses of skeletal parameters. Various authors have suggested different skeletal parameters to represent body weight in order to circumvent this problem. Radinsky (1968) suggests foramen magnum area as a suitable measurement, however, Gould (1975), Jerison (1973) and Martin (1973) have shown that foramen magnum area is influenced not only by body weight but also by brain size, thus rendering this measurement ambiguous. Gingerich (1974) suggests the length of the lower second molar, however, he subjectively excludes primate species with hypertrophied molars and, in addition, the interspecific correlation is not high.

Wood (1974) employs the length of the femur, however, this bone shows a high interspecific variability in length in the higher primates (Section V.2) Biegert and Mauer (1972) suggest the Skeletal Trunk Length (Rumpfskelettlange, Section III. 5) and demonstrate the high correlation of this measurement with the trunk length measurements taken on cadavars and ligamentous skeletons. These latter trunk length measurements have traditionally been used as measurements of body size in primatology and anthropology (Mollison, 1910, Schultz, 1929, Erikson, 1963, Washburn, 1942). These authors do not test the consistency of trunk length as a measure of body weight across their sample, however. The following allometric analysis tests this consistency and clearly shows that Skeletal Trunk Length is not a suitable measurement of body weight in the higher primates. This result is significant in view of the use of the Skeletal Trunk Length as the measurement of body weight in the published allometric analyses of limb proportions in the higher primates and brings into question the results of these analyses (Mauer, 1970/71, Biegart and Mauer, 1972, Halaczek, 1972).

IV. 3. The Relationship of Skeletal Trunk Length and Body Weight In the Higher Primates

Fig. IV.1 illustrates the bivariate relationship between Skeletal Trunk Length and body weight in the higher primates. Although the correlation coefficient is relatively high for the entire sample, there are at least two trends within this sample (Table IV.1). One is composed of the Group I primates and the second of the Group II primates. The least squares slope of the two samples are different at the 95% level of significance. In addition, each sex of species of primate making up the Group II sample lies outside the 95% confidence limits for primates of the same body weight on the projected Group I principal axis. Therefore, there is no constant relationship between body weight and Skeletal Trunk Length across the combined higher primate sample. If Skeletal Trunk Length is used indiscriminately as a measure of body weight in the higher primates, it can be expected

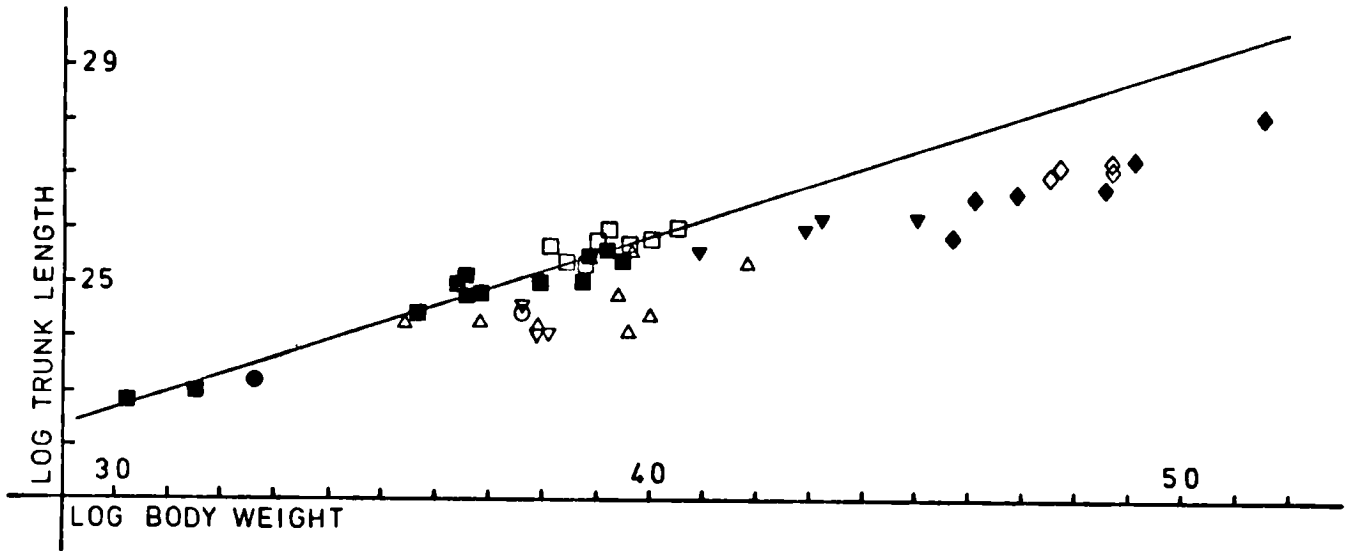

Fig. IV. 1. The relationship between body weight and skeletal trunk length.

Table IV.1.

X = LOG BODY WEIGHT Y = LOG TRUNK LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.32 (.29 - .36)	.23 (.17 + .28)	.21 (.19 - .23)
REDUCED MAJOR AXIS	.33	.24	.22
LEAST SQUARES Y.X	Y = 1.30+.32X	Y = 1.62+.22X	Y = 1.72+.21X
SLOPE & 95% C.L.	.32 ± .04	.22 ± .07	.21 ± .03
INTERCEPT & 95% C.L.	1.30 ± .15	1.62 ± .31	1.72 ± .10
LEAST SQUARES X.Y	X = -3.60+2.92Y	X = -5.47+3.80Y	Y = -7.04+4.34Y
SLOPE & 95% C.L.	2.92 ± .36	3.80 ± 1.13	4.34 ± .51
INTERCEPT & 95% C.L.	-3.60 ± .89	-5.47 ± 3.03	-7.04 ± 1.33
CORRELATION COEFFICIENT	.971	.921	.951
COEF. OF DETERMINATION	.943	.849	.904
UNEXPLAINED VARIANCE Y.X	.0005	.00078	.0014
UNEXPLAINED VARIANCE X.Y	.0044	.0133	.029
MEAN X	3.75	4.71	4.10
MEAN Y	2.51	2.68	2.57
SAMPLE SIZE	20	12	33

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

to confuse the interpretation of proportional relationships in these primates.

IV. 4. Measurements of the Cross Section of the Femur

Because limb bones are structural elements which must resist the force imposed by the weight of the body in motion, two measurements which reflect the strength of the limb were correlated with four standard measurements of the bone cross section. The idealised section modulus reflects the strength of the cross section in anterior posterior bending and the idealised cross sectional area reflects the strength of the bone in compression The four standard measurements are sagittal diameter, transverse diameter, circumference and average diameter. Table IV.2 gives the statistics for each comparison. It is apparent from the consistently high correlation coefficients that the four standard measurements of the femur cross section account for the maprity of the variance in each comparison. There is little additional information to be gained by employing either the section modulus or the cross sectional area in this type of interspecific comparison.

These high correlation coefficients do not necessarily mean that the four standard measurements directly represent the magnitude of strength in anterior-posterior bending or strength in compression, however. Only two out of the nine comparisons show an isometric increase with the strength measurements. Only the transverse diameter of the femur and the average diameter of the femur are isometric with bending strength. The sagittal diameter of the femur and circumference of the femur are significantly negatively allometric in relation to bending strength as are all four of the measurements in relation to the cross sectional area. These negatively allometric measurements do not increase in magnitude as rapidly as the bending or compressive strength of the bone cross section and, therefore, do not accurately represent the magnitude of the strength of the cross section. Models which simplistically employ these measurements in support of one or another theories of bone strength are, therefore, in error.

Table IV.2. Correlation coefficients and principal axes for the measurements of the cross section of the femur. Correlation coefficients are given in the upper right hand side of the table with the coefficients of determination in brackets beneath them. Principal axes are given in the lower left hand side of the table with the 95% confidence limits beneath them. An explanation of the abbreviations can be found in Appendix I.

Femur Cross Section Correlations and Principal Axes

	LFESEC	LFESD	LFETD	LFECIR	LFEAVD	LFEAVC	LWEIGHT	LFEAREA
LFESEC	*****	.997 (.995)	.993 (.986)	.998 (.997)	.999 (.999)	.989 (.979)	.988 (.976)	.999 (.997)
LFESD	.32 .31 - .33	*****				.982 (.965)	.978 (.956)	.993 (.987)
LFETD	.34 .32 - .35		*****			.983 (.966)	.992 (.984)	.994 (.988)
LFECIR	.32 .31 - .33			*****		.987 (.974)	.989 (.979)	.998 (.995)
LFEAVD	.33 ..32 - .33				*****	.986 (.973)		.998 (.995)
LFEAVC	.40 1.38 - .42	1.24 1.33 - 1.16	1.18 1.26 - 1.11	1.25 1.18 - 1.32	1.21 1.29 - 1.14	*****	.984 (.968)	.995 (.990)
LWEIGHT	1.17 1.11 - 1.24	.37 .35 - .40	.39 .38 - .41	.37 .35 - .39		.46 .43 - .49	*****	.991 (.983)
LFEAREA	.71 .69 - .72	2.20 2.11 - 2.29	2.10 2.02 - 2.18	2.21 2.16 - 2.27	2.15 2.10 - 2.20	1.78 1.72 - 1.84	.82 .79 - .86	*****

This negative allometric relationship can be explained by the average cortical thickness of the cross section. Table IV.2 also shows that cortical thickness is positively allometric in relation to both the femur section modulus and the femur average area, as well as in relation to the four external measurements. Therefore, the larger the cross section as measured by any of the four external measurements, the relatively larger the average cortical thickness will be. The positive allometry of the area of the femur in relation to the idealised section modulus also reflects this situation.

IV. 5. Measurements of the Cross Section of the Humerus

Table IV.3 provides similar information in relation to the cross section of the humerus. As with the femur, the high correlation coefficients indicate that the four standard measurements account for the great majority of the variance of both the humerus section modulus and the humerus average area, and, therefore, little additional information is gained by use of these more complicated measurements. However, reference to the principal axes in Table IV.3 shows that the four standard measurements with the exception of the average diameter of the humerus, are not isometric with either the humerus section modulus or the humerus average area. They, therefore, cannot be used to directly represent these measurements.

This lack of isometry cannot be explained with reference to a positive allometry of cortical thickness as with the femur, however. Table IV.3 indicates that cortical thickness is isometric with all of the cross sectional measurements except the humerus transverse diameter, with which it is positively allometric. The lack of isometry of the four standard measurements with humerus section modulus and humerus average area results from the lack of isometry of the sagittal diameter of the humerus and the transverse diameter of the humerus with each other. The humerus sagittal diameter increases significantly more rapidly than the humerus transverse diameter and, therefore, as the size of either the humerus sagittal

Table IV.3. Correlation coefficients and principal axes for the measurements of the cross section of the humerus.

Humerus Cross Section Correlations and Principal Axes

	LHUSEC	LHUSD	LHUTD	LHUCIR	LHUAVD	LHUAVC	LWEIGHT	LHUAREA
LHUSEC	*****	.997 (.995)	.992 (.984)	.998 (.996)	.999 (.999)	.985 (.970)	.987 (.975)	.998 (.997)
LHUSD	.35 .34 - .36	*****				.975 (.951)	.987 (.974)	.993 (.985)
LHUTD	.31 .29 - .32		*****			.979 (.958)	.977 (.955)	.993 (.987)
LHUCIR	.32 .31 - .32			*****		.981 (.963)	.986 (.971)	.998 (.995)
LHUAVD	.33 .32 - .33				*****	.981 (.963)		.997 (.995)
LHUAVC	.33 .31 - .35	1.05 .97 - 1.39	.92 .85 - .99	.95 .89 - 1.02	.98 .91 - 1.05	*****	.967 (.934)	.993 (.985)
LWEIGHT	1.16 1.10 - 1.23	.41 .38 - .43	.35 .33 - .38	.37 .34 - .39		.38 .35 - .42	*****	.984 (.968)
LHUAREA	.66 .64 - .67	.53 .51 - .56	.47 .45 - .49	.49 .47 - .50	.50 .49 - .51	.51 .49 - .53	.76 .71 - .81	*****

diameter or the humerus transverse diameter increases, the shape of the cross section becomes generally more ovoid. Because the humerus transverse diameter does not increase isometrically with the humerus sagittal diameter the section modulus does not increase as rapidly as does the humerus sagittal diameter. However, it increases much more rapidly than the humerus transverse diameter. The humerus average diameter does not increase as rapidly as does the humerus section modulus because the humerus transverse diameter is more negatively allometric than the humerus sagittal diameter is positively allometric. Therefore, the average of these will be negatively allometric. The circumference of the humerus is negatively allometric because it does not increase as rapidly as the humerus average diameter (Table IV.3). A similar explanation is true for the relationship between these measurements and the humerus average area.

Therefore, although the four standard measurements for both the cross section of the humerus and the cross section of the femur explain in excess of 98% of the variance of both the section modulus and the cross sectional area, the general lack of isometry of the standard measurements in relation to the strength measurements have different causes in the femur and in the humerus. In the femur, the positive allometry of the cortical thickness results in a more rapid increase of the femur section modulus and the femur average area in relation to the standard measurements. In the humerus, the positive allometry of the humerus sagittal diameter in relation to the humerus transverse diameter has a similar effect.

V. The Allometry of Bone and Limb Length in the Old World Monkeys, Apes and Human Beings

V. 1. Introduction

This chapter examines the allometry of bone length and limb length in relation to body weight in the Old World monkeys and apes. In addition, it also deals with the allometric relationships between the lengths of the different bones comprising the limbs. The primary purpose of these comparisons is to recognise the common trends in the various relationships and to recognise those species which are significantly different from these common trends.

V. 2. The Relationship Between Body Weight and the Length of the Femur

Fig. V.1. illustrates the relationship between body weight and the length of the femur in the Group 1 and Group 11 primates. The Group 1 primates show a fairly constant pattern of increase in femur length in relation to increase in body size. The correlation coefficient is high and the principal axis is just not significantly different from isometry (Table V.1). Both sexes of Papio anubis clearly belong to this trend, while both Gorilla and Pongo deviate from this trend in the direction of a short femur for their body weights. It is not obvious, however, whether or not Hylobates mulleri, Homo sapiens and Pan belong to the Group 1 trend in this relationship. When these species are tested for inclusion in this trend both Pan and Hylobates are significantly different at the 95% level of significance. Hylobates has a significantly longer femur for its body weight, while Pan has a significantly shorter femur for its body weight than would be expected on the basis of this trend. The position of Homo sapiens is ambiguous. When the body weight is considered to be the dependent variable and femur length the independent variable, both sexes of both races of Homo sapiens are not significantly different from the expectations based on the Group 1 trend. However, when body weight is taken as the independent variable and the length of the femur as the dependent variable, both the male and the female negroes are significantly different from the trend, while the male and female caucasians are not significantly different from

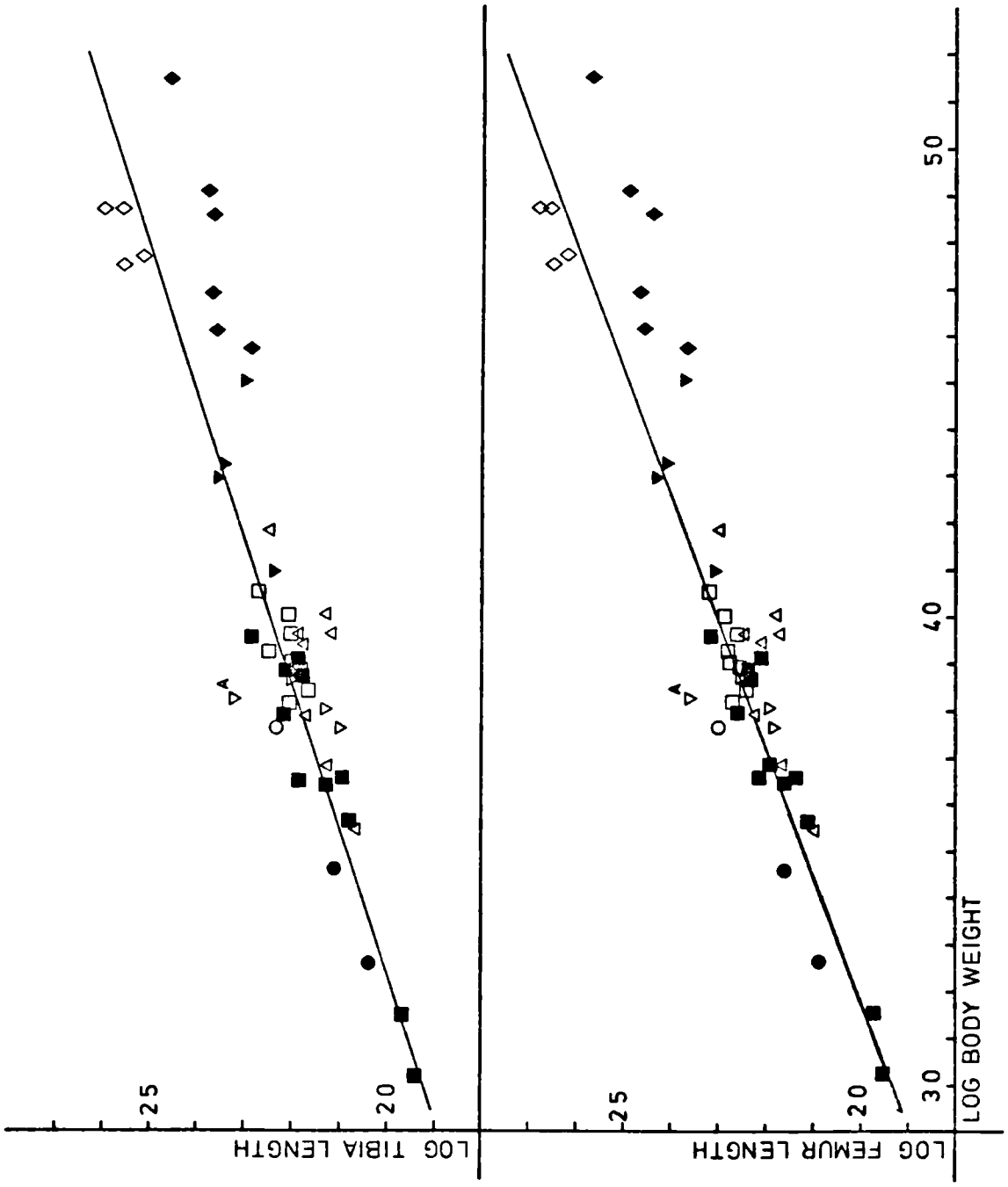
LOG TIBIA LENGTH
25
20
LOG FEMUR LENGTH
25
20
30
40
50
LOG BODY WEIGHT

Fig. V.2.

Fig. V.1.

Table V.1.

X = LOG BODY WEIGHT Y = LOG FEMUR LENGTH

	GROUP 1
PRINCIPAL AXIS	.37 (.33 - .41)
REDUCED MAJOR AXIS	.38
LEAST SQUARES Y.X	Y = .83+.37X
SLOPE & 95% C.L.	.37 ±
INTERCEPT & 95% C.L.	.83 ±
LEAST SQUARES X.Y	X = -1.87+2.54Y
SLOPE & 95% C.L.	2.54 ± .33
INTERCEPT & 95% C.L.	-1.87 ± .72
CORRELATION COEFFICIENT	.968
COEF. OF DETERMINATION	.937
UNEXPLAINED VARIANCE Y.X	.0007
UNEXPLAINED VARIANCE X.Y	.0047
MEAN X	3.76
MEAN Y	2.21
SAMPLE SIZE	20

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

it. However, male and female negroes are closer to the trend than are Hylobates, Pan or the more extreme Pongo or Gorilla. It is clear also that Pan and Gorilla do not lie on the same intraspecific trend, Gorilla is further derived in the reduction of the femur relative to body size than is Pan.

V. 3. The Relationship Between Body Weight and the Length of the Tibia

The relationship between body weight and the length of the tibia is similar to the relationship between body weight and the length of the femur in the Group 1 and Group 11 primates (Fig. V.2). The principal axis for the relationship between body weight and the length of the tibia is lower than that for the relationship between body weight and the length of the femur. However, the difference between these principal axes is not significant at the 95%level of confidence (Tables V.1 and V.2). On the basis of these comparisons it must be concluded that both the tibia and femur increase in length in an essentially similar fashion in relation to body weight increase within the Group 1 primates. However, this conclusion is not clearly supported by the relationship between the length of the femur and the length of the tibia (Section V.4). This relationship clearly shows a significantly greater increase in the length of the femur in relation to the length of the tibia in the Group 1 primates, as well as in the entire Group 1 and Group 11 sample. The ambiguity of these comparisons illustrates the problems involved in using statistical tests of significance on biological data. The variation in the length of both these bones in relation to body weight in the Group 1 primates masks the highly constant positive allometric relationship between femur length and tibia length in these primates.

The relationship of the Group 11 primates to the Group 1 trend in the comparison between body weight and the length of the tibia is similar to their relationship in comparison between the body weight and the length of the femur. Hylobates has a significantly longer tibia than would be expected on the basis of this trend, while Pan, Pongo and Gorilla have significantly

Table V.2.

X = LOG BODY WEIGHT Y = LOG TIBIA LENGTH

	GROUP 1
PRINCIPAL AXIS	.33 (.27 - .38)
REDUCED MAJOR AXIS	.34
LEAST SQUARES Y.X	Y = .97+.32X
SLOPE & 95% C.L.	.32 ± .06
INTERCEPT & 95% C.L.	.97 ± .22
LEAST SQUARES X.Y	X = -2.39+2.83Y
SLOPE & 95% C.L.	2.83 ± .52
INTERCEPT & 95% C.L.	-2.39 ± 1.12
CORRELATION COEFFICIENT	.953
COEF. OF DETERMINATION	.908
UNEXPLAINED VARIANCE Y.X	.0009
UNEXPLAINED VARIANCE X.Y	.0080
MEAN X	3.75
MEAN Y	2.17
SAMPLE SIZE	16

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

shorter tibia than would be expected. Homo sapiens is not significantly different from the Group 1 trend in this comparison. Although the Homo sapiens negro females have an observed body weight which falls outside of the 95% confidence limits for the expected body weight predicted from tibia length based on the Group 1 analysis, they are just barely outside these limits.

V. 4. The Relationship Between the Length of the Femur and the Length of the Tibia

Fig. V.3 illustrates the relationship between the length of the femur and the length of the tibia in the Group 1 and Group 11 primates. The principal axis is positive and the correlation coefficient is very high (Table V.3). This is true, irrespective of whether or not the femur and the tibia are long in relation to body weight (as in Hylobates), or short in relation to body weight (as in Pan, Pongo and Gorilla). The high correlation of the relationship between the length of the femur and the length of the tibia across the entire Group 1 and Group 11 sample makes it possible to predict the length of one of these bones from the length of the other. This could be of particular importance in the reconstruction of, for example, the length of a fragmentary tibia when the length of the associated femur is known. This would, thereby, provide a reasonable estimate of the length of the entire lower limb.

V. 5. The Relationship Between Body Weight and the Crural Index

Fig. V.4 illustrates the relationship between body weight and the crural index in the Group 1 and Group 11 primates. The principal axis characterising this relationship is significantly negative (Table V.4). Therefore, with increasing body weight the crural index decreases. However, there are a few species, such as Cercopithecus mitis, Cercocebus albigena and Homo sapiens, in which the males have a crural index equal to, or higher than, the females. This suggests that the decrease in the crural index with body weight increase is an interspecific, and not an intraspecific, phenomenon across the sample.

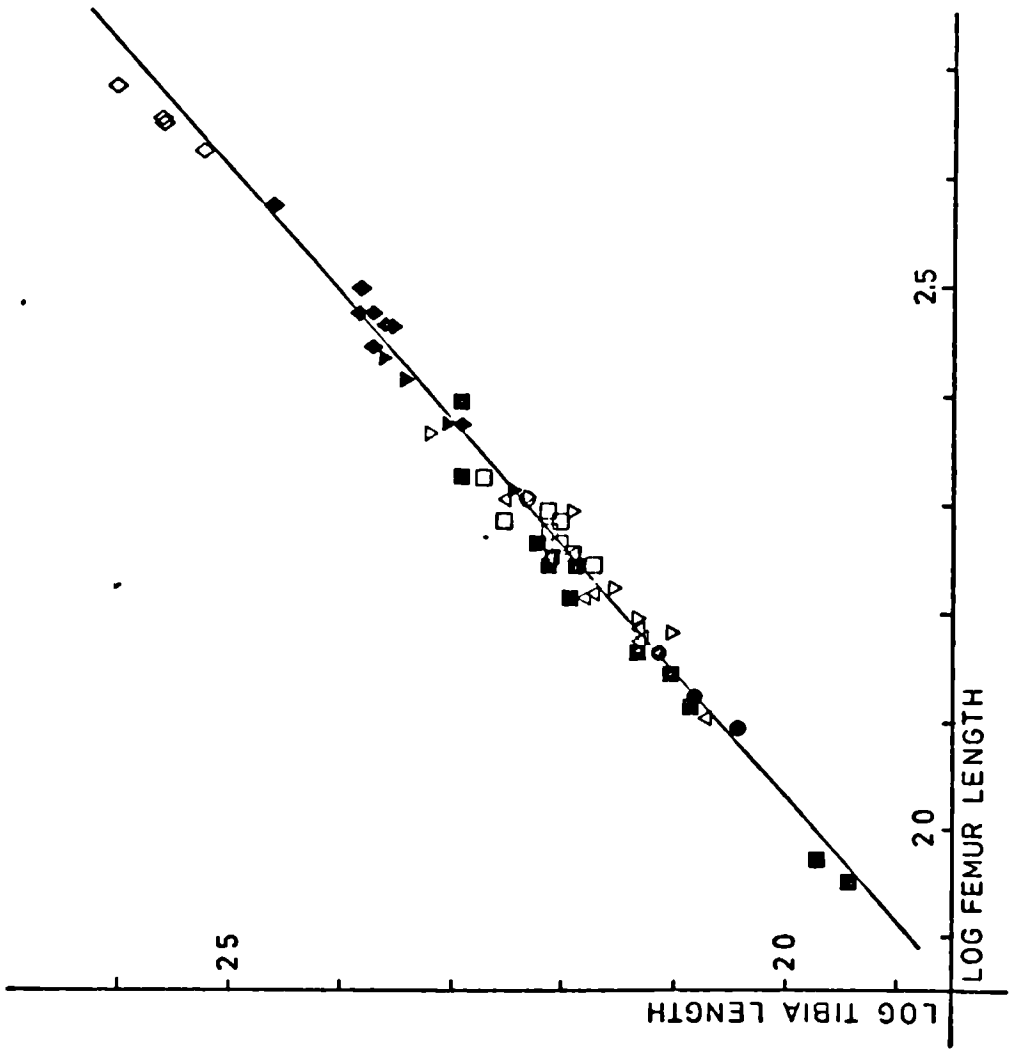

Fig. V.3.

Table V.3.

X = LOG FEMUR LENGTH Y = LOG TIBIA LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.89 (.83 - .95)	.94 (.88 - 1.00)	.86 (.84 - .89)
REDUCED MAJOR AXIS	.89	.94	.86
LEAST SQUARES Y.X	Y = .22+.88X	Y = .07+.94X	Y = .27+.86X
SLOPE & 95% C.L.	.88 ± .07	.94 ± .07	.86 ± .03
INTERCEPT & 95% C.L.	.22 ± .15	.07 ± .19	.27 ± .07
LEAST SQUARES X.Y	X = -.20+1.11Y	X = -.04+1.06Y	X = -.29+1.15Y
SLOPE & 95% C.L.	1.11 ± .09	1.06 ± .08	1.15 ± .04
INTERCEPT & 95% C.L.	-.20 ± .19	-.04 ± .20	-.29 ± .09
CORRELATION COEFFICIENT	.990	.994	.996
COEF. OF DETERMINATION	.981	.988	.992
UNEXPLAINED VARIANCE Y.X	.00019	.00018	.0002
UNEXPLAINED VARIANCE X.Y	.00024	.0002	.00028
MEAN X	2.22	2.51	2.33
MEAN Y	2.18	2.42	2.27
SAMPLE SIZE	17	12	29

GROUP 1 — COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 — PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 — GROUP 1 AND GROUP 2

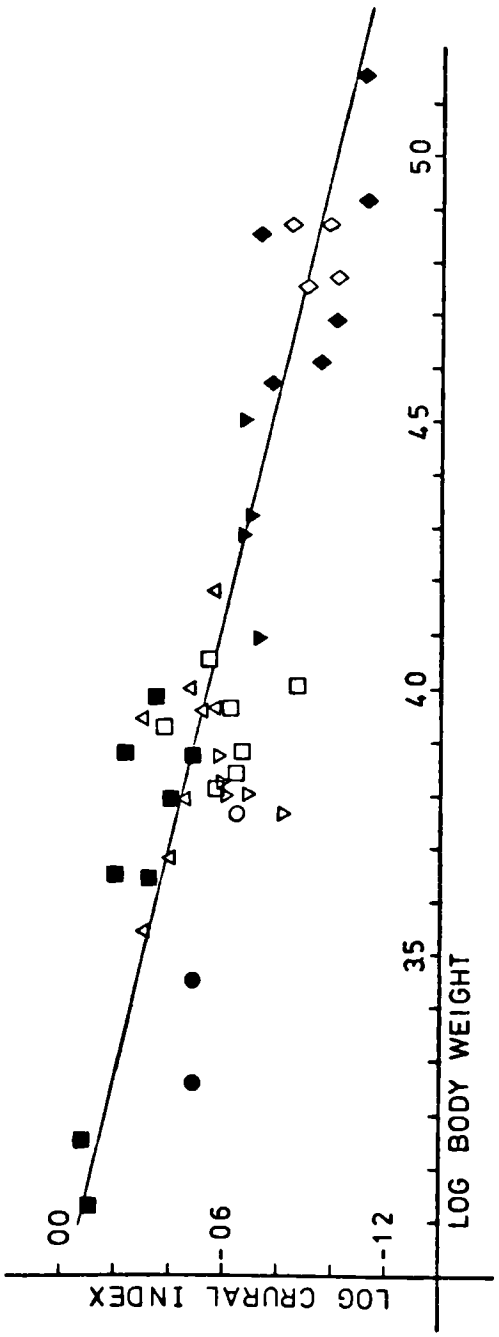

Fig. V.4. The relationship between body weight and the crural index.

Table V.4.

X = LOG BODY WEIGHT Y = LOG CRURAL INDEX

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	-.04 (-.07 - -.02)	-.04 (-.06 - -.01)	-.05 (-.06 - -.04)
REDUCED MAJOR AXIS	.07	.05	.06
LEAST SQUARES Y.X	Y = .13-.04X	Y = .08-.04X	Y = .15-.05X
SLOPE & 95% C.L.	-.04 ± .03	-.04 ± .03	-.05 ± .01
INTERCEPT & 95% C.L.	.13 ± .11	.08 ± .13	.15 ± .04
LEAST SQUARES X.Y	X = 3.36-10.14Y	X = 3.59-12.26Y	X = 3.19-16.05Y
SLOPE & 95% C.L.	-10.14 ± 6.52	-12.26 ± 9.91	-16.05 ± 3.01
INTERCEPT & 95% C.L.	3.36 ± .28	3.59 ± .91	3.19 ± .10
CORRELATION COEFFICIENT	-.666	-.658	-.907
COEF. OF DETERMINATION	.443	.432	.823
UNEXPLAINED VARIANCE Y.X	.0002	.00014	.00018
UNEXPLAINED VARIANCE X.Y	.0486	.0494	.0569
MEAN X	3.75	4.71	4.16
MEAN Y	-.04	-.09	-.06
SAMPLE SIZE	16	12	28

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

V. 6. The Relationship Between Body Weight and the Length of the Hindlimb

Fig. V.5 illustrates the relationship between hindlimb length (femur length + tibia length) and body weight in the Group 1 and Group 11 primates. The principal axis for this relationship in the Group 1 sample is clearly isometric (Table V.5).

As in the previous comparisons between the length of the femur and body weight and the length of the tibia and body weight, Hylobates is significantly different from the Group 1 trend in the direction of a longer hindlimb for its body weight. Pan, Gorilla and Pongo are also significantly different from this trend, but in the direction of a short hindlimb for their body weights. Gorilla and Pongo have equally short hindlimbs relative to their body weights, while Pan has a longer hindlimb than do these other apes. The caucasian Homo sapiens are not significantly different from the Group 1 trend. However, the female negro Homo sapiens lies slightly outside the 95% confidence limits in the comparisons.

V. 7. The Relationship Between Body Weight and the Length of the Humerus

Fig. V.6 illustrates the relationship between body weight and the length of the humerus in Group 1 and Group 11 primates. The principal axis for the entire sample is significantly positive and the correlation coefficient is high (Table V.6). The principal axis for the Group 1 primates is not significantly different from the principal axis for the Group 11 primates. Therefore, there is no statistical reason to suggest that there is more than one allometric trend for this relationship characterising the entire sample. It must be noted, however, that this conclusion is not supported by the relationship between the length of the humerus and the length of the femur in section V.8.

The only primate which is significantly different from the remaining sample in the relationship between body weight and the length of the humerus is Hylobates. This primate has an exceptionally long humerus in relation to its body weight.

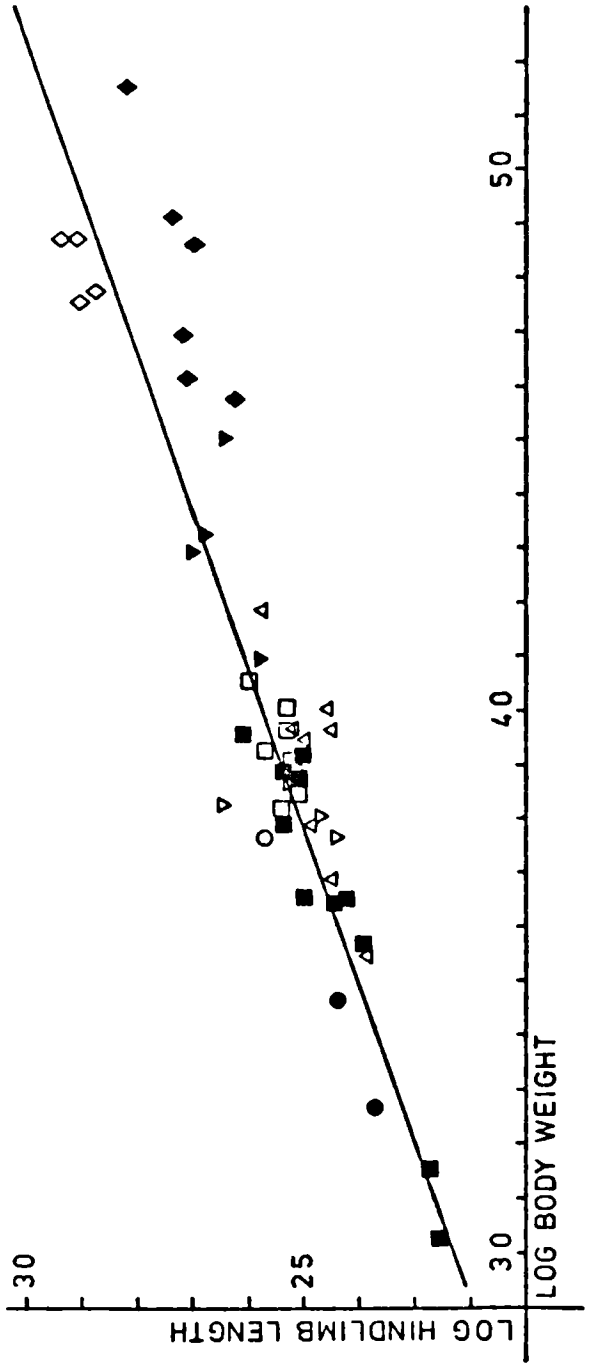

Fig. V.5. The relationship between body weight and the length of the hindlimb.

Table V.5.

X = LOG BODY WEIGHT Y = LOG HINDLIMB LENGTH

	GROUP 1
PRINCIPAL AXIS	.35 (.30 - .40)
REDUCED MAJOR AXIS	.35
LEAST SQUARES Y.X	Y = 1.20+.35X
SLOPE & 95% C.L.	.35 ± .06
INTERCEPT & 95% C.L.	1.20 ± .21
LEAST SQUARES X.Y	X = -2.93+2.68Y
SLOPE & 95% C.L.	2.68 ± .44
INTERCEPT & 95% C.L.	-2.93 ± 1.09
CORRELATION COEFFICIENT	.962
COEF. OF DETERMINATION	.952
UNEXPLAINED VARIANCE Y.X	.00084
UNEXPLAINED VARIANCE X.Y	.0065
MEAN X	3.75
MEAN Y	2.49
SAMPLE SIZE	16

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

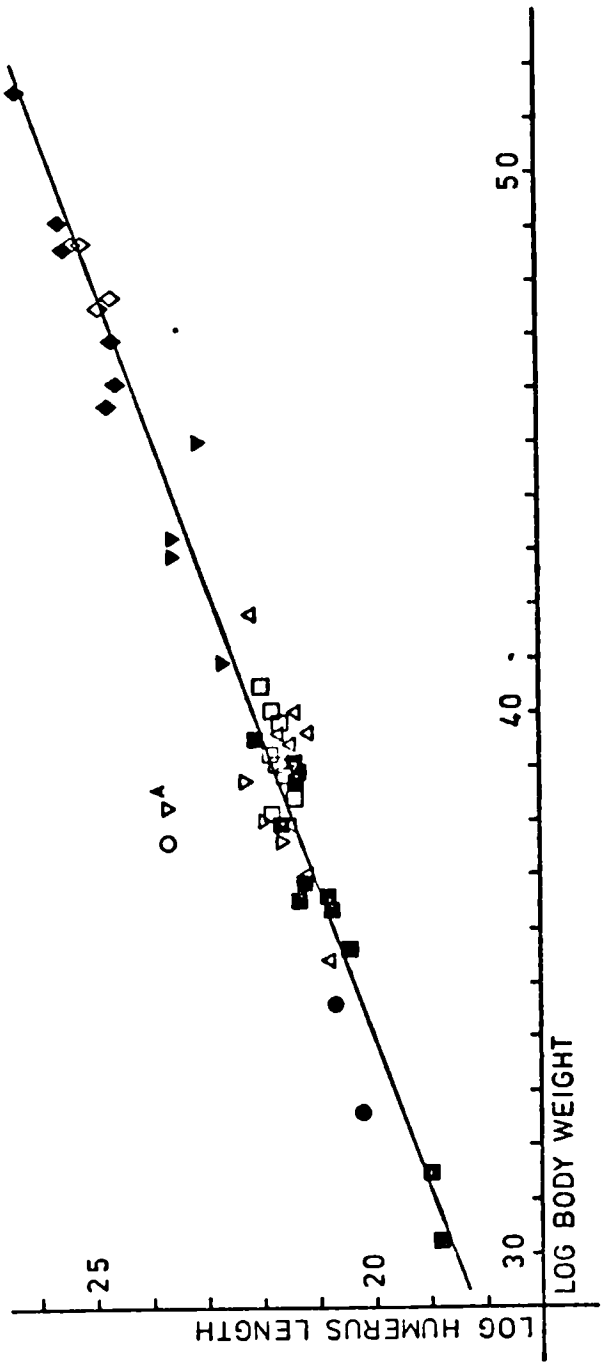

Fig. V.6. The relationship between body weight and the length of the humerus.

Table V.6.

X = LOG BODY WEIGHT Y = LOG HUMERUS LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.33 (.30 - .37)	.33 (.30 - .37)	.37 (.36 - .39)
REDUCED MAJOR AXIS	.34	.34	.37
LEAST SQUARES Y.X	Y = .89+.33X	Y = .94+.33X	Y = .74+.37X
SLOPE & 95% C.L.	.33 ± .04	.33 ± .05	.37 ± .02
INTERCEPT & 95% C.L.	.89 ± .15	.94 ± .22	.74 ± .07
LEAST SQUARES X.Y	X = -2.36+2.89Y	X = -2.57+2.93Y	X = -1.91+2.67Y
SLOPE & 95% C.L.	2.89 ± .34	2.93 ± .41	2.67 ± .12
INTERCEPT & 95% C.L.	-2.36 ± .73	-2.57 ± 1.02	-1.91 ± .26
CORRELATION COEFFICIENT	.973	.982	.993
COEF. OF DETERMINATION	.946	.964	.986
UNEXPLAINED VARIANCE Y.X	.00046	.00036	.00058
UNEXPLAINED VARIANCE X.Y	.0040	.0032	.0042
MEAN X	3.76	4.71	4.10
MEAN Y	2.12	2.49	2.25
SAMPLE SIZE	20	12	33

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

V. 8. The Relationship Between the Length of the Humerus and the Length of the Femur

Fig. V.7 illustrates the relationship between the length of the humerus and the length of the femur in the Group 1 and Group 11 primates. The principal axis for the Group 1 primates is significantly positive (Table V.7).

However, this principal axis is inconsistent with the data which has already been presented for the relationship between the length of the femur and body weight and for the relationship between the length of the humerus and body weight (Sections V.2 and V.7). Table V.8 gives the expected principal axis for the relationship between humerus length and femur length based on the results of the comparisons of the two bone lengths with body weight. This expected principal axis is virtually isometric, and lies outside the 95% confidence limits for the observed relationship between these two bone lengths presented in the previous sections. The discrepancy appears to lie with the relationship between body weight and humerus length. If the principal axis for the relationship between body weight and the length of the humerus is computed only on the basis of the Group 1 primates, it is considerably lower than the principal axis for the combined Group 1 and Group 11 sample. However, it still falls within the 95% confidence limits for the principal axis of the combined Group 1 and Group 11 sample. Although it is not statistically justifiable to separate the Group 1 primates from the Group 11 primates in the relationship between body weight and the length of the humerus, the isometric principal axis for the Group 1 primates is consistent with the observed principal axis for the relationship between the length of the femur and the length of the humerus. Therefore, the relationship between femur length and humerus length provides strong evidence against the conclusion that there is one positive trend which characterises the relationship between body weight and humerus length in both the Group 1 and the Group 11 primates.

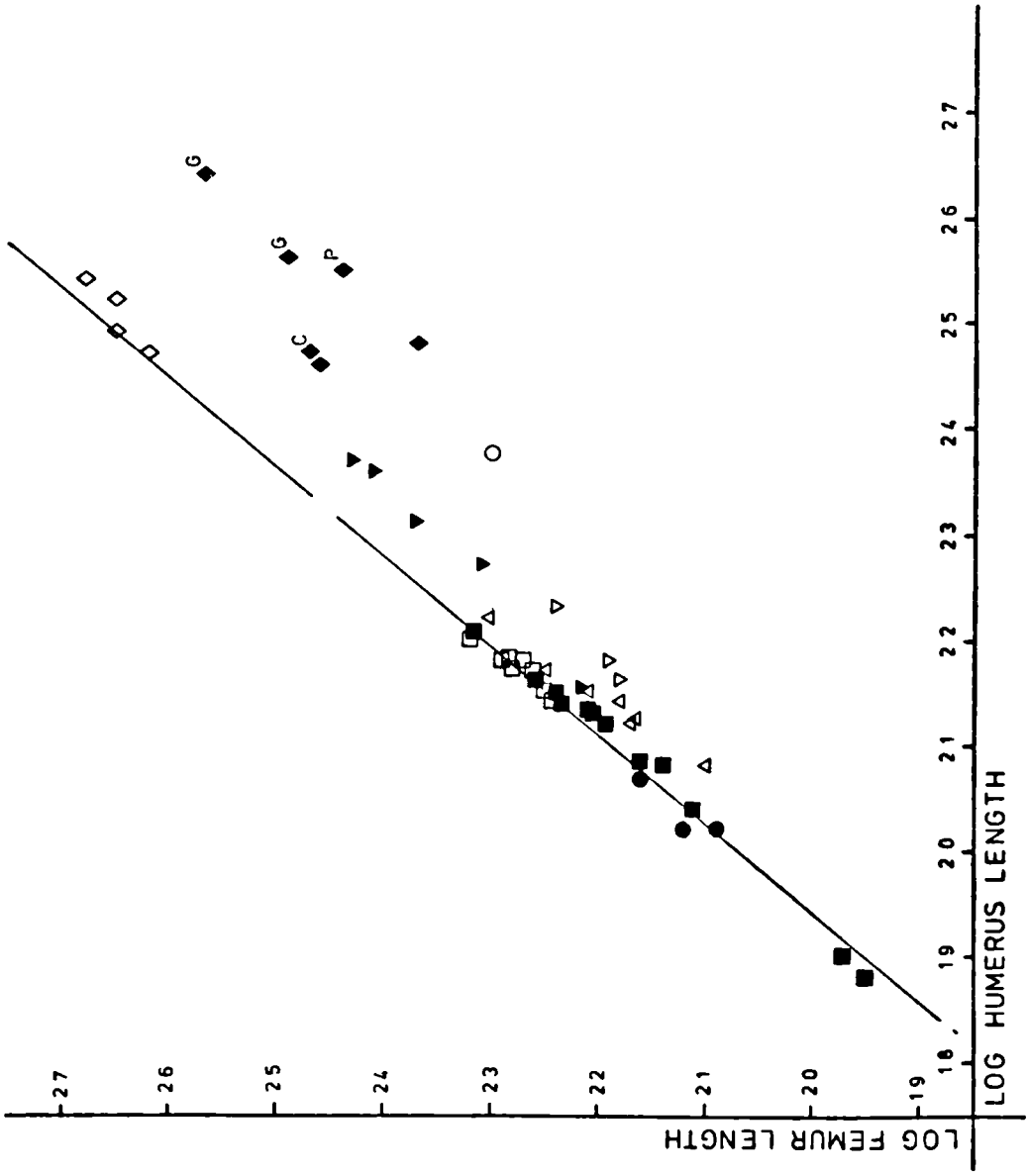

Fig. V.7. The relationship between the length of the humerus and the length of the femur.

Table V.7.

X = LOG HUMERUS LENGTH Y = LOG FEMUR LENGTH

	GROUP 1
PRINCIPAL AXIS	1.18 (1.07 - 1.30)
REDUCED MAJOR AXIS	1.17
LEAST SQUARES Y.X	Y = -.20+1.14X
SLOPE & 95% C.L.	1.14 ± .13
INTERCEPT & 95% C.L.	-.20 ± .27
LEAST SQUARES X.Y	X = .28+.83Y
SLOPE & 95% C.L.	.83 ± .09
INTERCEPT & 95% C.L.	.28 ± .21
CORRELATION COEFFICIENT	.974
COEF. OF DETERMINATION	.949
UNEXPLAINED VARIANCE Y.X	.0006
UNEXPLAINED VARIANCE X.Y	.0004
MEAN X	2.12
MEAN Y	2.22
SAMPLE SIZE	21

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

Table V.8. -- The expected principal axis compared to the observed principal axis for the relationship between the length of the humerus and the length of the femur

I. Observed relationship between bone length and body weight

log femur length = .37 log body weight (Table V.2)

log humerus length = .37 log body weight (Table V.6)*

Expected relationship between the length of the femur and the length of the humerus based on observed relationships I

log femur length = 1.00 log humerus length

II. Observed relationship between bone length and body weight

log femur length = .37 log body weight (Table V.2)

log humerus length = .33 log body weight (Table V.6)**

Expected relationship between the length of the femur and the length of the humerus based on observed relationships II

log femur length = .37/.33 log humerus length

log femur length = 1.12 log humerus length

III. Observed relationship between the length of the femur and the length of the humerus

log femur length = 1.18 log humerus length

(95% confidence limits for the observed principal axis = 1.07 - 1.30)

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* postive principal axis of the combined Group 1 and Group 2 primates assumed to be characteristic of the Group 1 primates alone.

** isometric principal axis taken as the accurate characterization of the Group I relationship between the length of the humerus and body weight.

Based on this evidence the possibility must be entertained that statistical significance does not necessarily correspond to biological significance in allometric analysis. The relationship between the length of the femur and the length of the humerus supports the hypothesis that there are at least two trends in the relationship between body weight and humerus length in the Group 1 and Group 11 primates, irrespective of the statistical conclusions.

The following conclusions can be drawn on the basis of the relationship between the length of the femur and the length of the humerus

1. Within the Group 1 primates the femur length increases at a more rapid rate relative to body weight than does the humerus length.
2. Papio anubis has a significantly longer humerus in in relation to the length of its femur than would be expected within the Group 1 trend.
3. The long humerus relative to the length of the femur in Pan, Gorilla and Pongo is primarily a function of of the short femur in relation to body weight in these primates. It cannot be explained by an unusually long humerus in relation to body weight.
4. In Hylobates, both the femur and the humerus are significantly long in relation to body weight (Sections V.2 and V.7). However, the humerus is much more elongated in relation to body weight than is the femur.
5. Homo sapiens is not significantly different from the Group 1 trend.

V. 9. The Relationship Between Body Weight and the Length of the Radius

Fig. V.8 illustrates the relationship between body weight and the length of the radius in the Group 1 and Group 11 primates. This relationship differs from the relationship between body weight and the length of the humerus (Section V.7) in two ways. Firstly, the principal axis for this relationship is isometric (Table V.9),

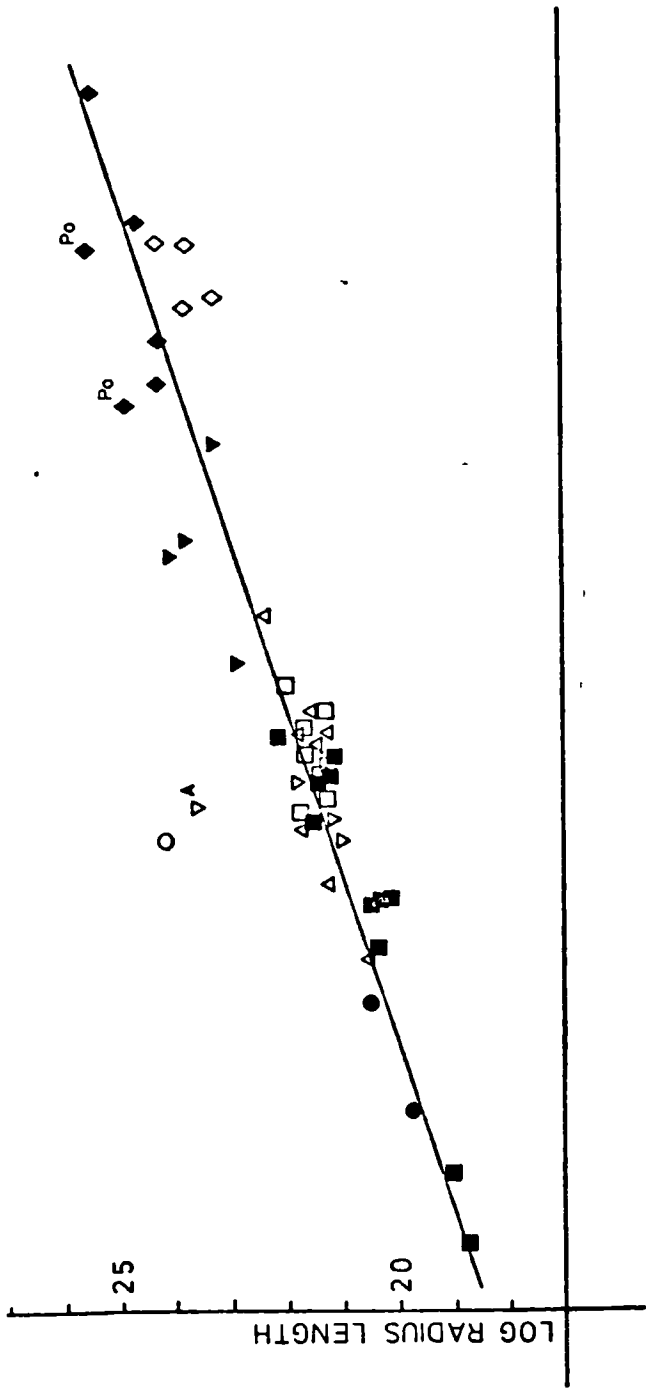

Fig. V.8. The relationship between body weight and the length of the radius.

Table V.9.

X = LOG BODY WEIGHT Y = LOG RADIUS LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.33 (.28 - .38)	.19 (.06 - .32)	.32 (.28 - .35)
REDUCED MAJOR AXIS	.34	.28	.33
LEAST SQUARES Y.X	Y = .89+.33X	Y = 1.58+.18X	Y = .93+.32X
SLOPE & 95% C.L.	.33 ± .06	.18 ± .16	.32 ± .04
INTERCEPT & 95% C.L.	.89 ±	1.58 ± .74	.93 ± .16
LEAST SQUARES X.Y	X = -2.19+2.82Y	X = -.81+2.27Y	X = -2.40+2.92Y
SLOPE & 95% C.L.	2.82 ± .49	2.27 ± 1.96	2.92 ± .34
INTERCEPT & 95% C.L.	-2.19 ± 1.04	-.81 ± 4.78	-2.40 ± .77
CORRELATION COEFFICIENT	.957	.641	.960
COEF. OF DETERMINATION	.915	.411	.922
UNEXPLAINED VARIANCE Y.X	.00085	.0041	.0027
UNEXPLAINED VARIANCE X.Y	.0074	.0516	.0252
MEAN X	3.75	4.71	4.16
MEAN Y	2.11	2.43	2.25
SAMPLE SIZE	16	12	28

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

while the principal axis in the humerus length comparison is significantly positive (Table V.6). Secondly, there is a significantly lower correlation coefficient as well as a significantly greater amount of the variance left unexplained in this relationship than there is in the relationship between body weight and the length of the humerus (Tables V.6 and V.9). It is clear that these differences are due to variation in the Group II primates and not in the Group I primates. When the principal axes and the unexplained variances for the two subsamples in the two allometric comparisons are compared, both the principal axis and the unexplained variance are identical for the Group I primates. For the Group II primates, the principal axis is significantly lower in the radius length comparison than it is in the humerus length comparison. There is also a significantly greater amount of unexplained variance. Therefore, it can be concluded that the radius behaves in relation to body weight in a similar fashion to the humerus in the Group I primates, but not in the Group II primates. Comparison of Fig. V.6 and Fig. V.8 suggests that the lower principal axis and the increased unexplained variance in the radius length comparison results from the positions of Pan, Gorilla and Homo. These primates have a radius which is short in relation to their body weights in comparison to the relationship between their humerus lengths and their body weights.

As in the comparison between body weight and the length of the humerus (Section V.7) there is one outlying group in the comparison between body weight and the length of the radius. Hylobates shows a greater deviation in the length of its radius in relation to the Group I primates than it does in the length of its humerus in relation to this trend (Fig. V.6). This suggests that the elongation of the forelimb in Hylobates has involved the radius to a greater degree than it has the humerus.

V. 10. The Relationship Between the Length of the Humerus and the Length of the Radius

Fig. V.9 illustrates the relationship between the length of the humerus and the length of the radius in the Group 1 and Group 11 primates. The principal axis for the Group 1 primates is isometric (Table V.10). Pongo is not significantly different from the trend, while Hylobates, Gorilla and Homo are significantly different. Hylobates has a longer radius in relation to its humerus length than would be expected from the Group 1 trend , and both Gorilla and Homo have shorter radii in relation to their humerus length than would be expected on the basis of this trend. The position of both Papio anubis and Pan are ambiguous. When the length of the radius is tested against the length of the humerus (radius length is considered the dependent variable and the humerus length the independent variable for the sake of the analysis) both sexes of Papio anubis and Pan (female) are just significantly different from the predictions of the Group 1 trend, while Pan (male) is just not significantly different. However, when the length of the humerus is tested against the length of the radius (radius length considered the independent variable and humerus length the dependent variable) both sexes of Papio anubis are not significantly different from the Group 1 trend, while both sexes of Pan are significantly different.

Therefore, in relation to the Group 1 trend which shows an isometric increase of the radius length in relation to the humerus length, both Hylobates and Papio can be considered to be specialised in having a radius longer than the expectation while Pan, Gorilla and Homo are specialised in having a radius shorter than this trend. In addition, Papio anubis is ambiguous.

There is an alternative interpretation for the increase in the length of the radius in relation to the length of the humerus, however. There is a highly correlated positive relationship between these variables in the Group 1 sample when Cercopithecus talapoin is excluded from the analysis. This positive relationship is significantly different from the isometric interpretation in

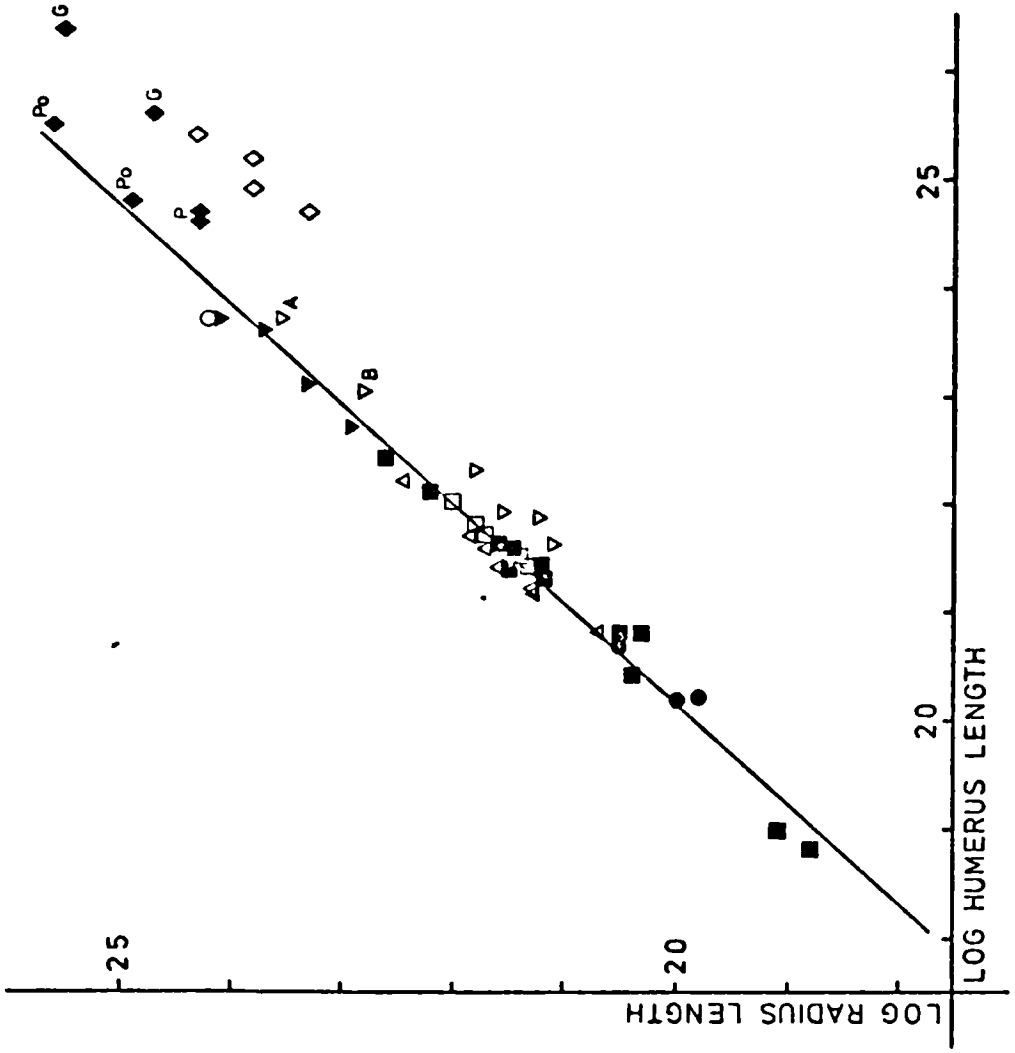

Fig. V.9.
The relationship between the length of the humerus and the length of the radius.

Table V.10

X = LOG HUMERUS LENGTH Y = LOG RADIUS LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	1.02 (.95 - 1.10)	1.30 (1.20 - 1.41)	1.05 (.98 - 1.14)
REDUCED MAJOR AXIS	1.02	1.30	1.05
LEAST SQUARES Y.X	Y = -.03+1.01X	Y = -.61+1.28X	Y = -.09+1.04Y
SLOPE & 95% C.L.	1.01 ± .09	1.28 ± .12	1.04 ± .09
INTERCEPT & 95% C.L.	-.03 ± .18	-.61 ± .26	-.09 ± .19
LEAST SQUARES X.Y	X = -.08+.97Y	X = .52+.76Y	X = .15+.94Y
SLOPE & 95% C.L.	.97 ± .08	.76 ± .07	.94 ± .08
INTERCEPT & 95% C.L.	.08 ± .17	.52 ± .16	.15 ± .17
CORRELATION COEFFICIENT	.989	.987	.984
COEF. OF DETERMINATION	.978	.974	.969
UNEXPLAINED VARIANCE Y.X	.00025	.000087	.00040
UNEXPLAINED VARIANCE X.Y	.00024	.000052	.00036
MEAN X	2.13	2.16	2.14
MEAN Y	2.12	2.15	2.14
SAMPLE SIZE	17	15	22

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 Group 1 minus Cercopithecus talapoin

GROUP 3 Group 1 plus Papio anubis

the previous discussion. The principal axis for this trend is positively allometric (Table V.10), indicating a marked tendency for the radius to increase in length relative to an increase in the length of the humerus. The reality of a positive trend in the relationship between the length of the humerus and the length of the radius in the primates is supported by the following evidence

1. There is a significantly higher correlation coefficient associated with the positive trend than there is with the isometric trend.
2. There is a significantly greater amount of the variance explained by the positive trend than there is by the isometric trend (Table V. 10).

If the positive trend is a valid interpretation of the relationship between humerus length and radius length, there are some interesting implications for the Group 11 primates

1. Hylobates falls on the extension of this positive trend. It is possible that the exceedingly long forelimb in this species is the result of an acceleration of growth within a basic Group 1 pattern. This would offer an explanation for the greater participation of the radius in the lengthening of the forelimb than of the humerus. In order to clearly support this hypothesis, a larger sample of Hylobates and Symphalangus species would be required, as well as detailed growth studies on the relevant species.
2. Cercopithecus talapoin shows a longer radius in relation to its humerus length than would be expected. It is possible that this is an adaptation to maintain an efficient arboreal quadrupedal locomotion at a small body size. If Cercopithecus talapoin is a dwarfed species, and it it had adhered to the positive allometric Group 1 trend, the radius, and therefore, the forelimb, would be extremely short. This primate could be dwarfed along an isometric trend.

V. 11. The Relationship Between Body Weight and the Brachial Index

Fig. V. 10 illustrates the relationship between body weight and the brachial index in the Group 1 and Group 11 primates. This comparison summarises the majority of the points in the previous discussions of the individual bones composing the forelimb.

1. There is no significant correlation between body weight and the brachial index in the Group 1 primates (Table V. 11). This reflects the basic isometric relationship between body weight and radius length and body weight and humerus length in these species. The marginal position of Pan reflects its marginal position in the isometric interpretation of the relationship between humerus length and radius length.
2. There is a significant positive correlation between body weight and the brachial index within the Group 1 primates when Cercopithecus talapoin is excluded from the sample. This reflects the strongly positive relationship of the length of the humerus and the length of the radius in these primates. This positive allometric relationship must be viewed as an interspecific, rather than an intraspecific, phenomenon, however.
3. The position of Gorilla and Homo sapiens in this comparison directly reflects the extreme shortening of the radius in relation to body weight and in relation to humerus length in these primates.

V. 12. The Relationship Between the Length of the Tibia and the Length of the Radius

Fig. V. 11 illustrates the relationship between the length of the radius and the length of the tibia in the Group 1 and Group 11 primates. The principal axis for the Group 1 primates is isometric (Table V. 12). This reflects the isometric relationship of both the length of the tibia and the length of the radius with body weight. The positions of the individual Group 11 primates

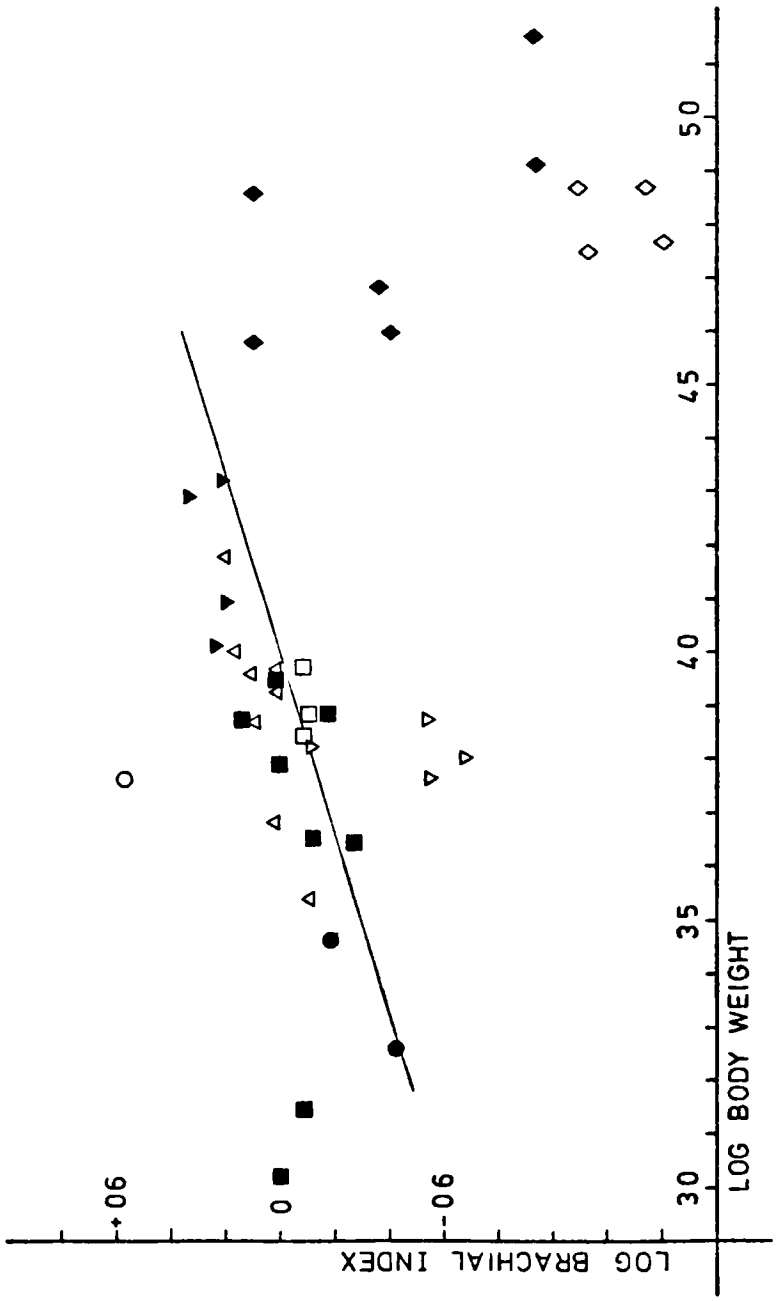

Fig. V.10. The relationship between body weight and the brachial index.

Table V.11.

X = LOG BODY WEIGHT Y = LOG BRACHIAL INDEX

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	-.01 (-.03 - .02)	.06 (.01 - .11)	.01 (-.01 - .03)
REDUCED MAJOR AXIS	.05	.11	.05
LEAST SQUARES Y.X	Y = .01-.01X	Y = -.25+.06X	Y = -.05+.01X
SLOPE & 95% C.L.	-.01 ± .03	.06 ± .06	.01 ± .03
INTERCEPT & 95% C.L.	.01 ± .11	-.25 ± .24	-.05 ± .10
LEAST SQUARES X.Y	X = 3.73-1.96Y	X = 3.89+4.72Y	X = 3.82+3.92Y
SLOPE & 95% C.L.	-1.96 ± 11.41	4.72 ± 4.61	3.92 ± 9.74
INTERCEPT & 95% C.L.	3.73 ± .18	3.89 ± .08	3.82 ± .16
CORRELATION COEFFICIENT	-.098	.54	.209
COEF. OF DETERMINATION	.010	.29	.044
UNEXPLAINED VARIANCE Y.X	.0002	.00016	.0003
UNEXPLAINED VARIANCE X.Y	.0865	.012	.0969
MEAN X	3.75	3.84	3.80
MEAN Y	-.008	-.01	.005
SAMPLE SIZE	16	14	18

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

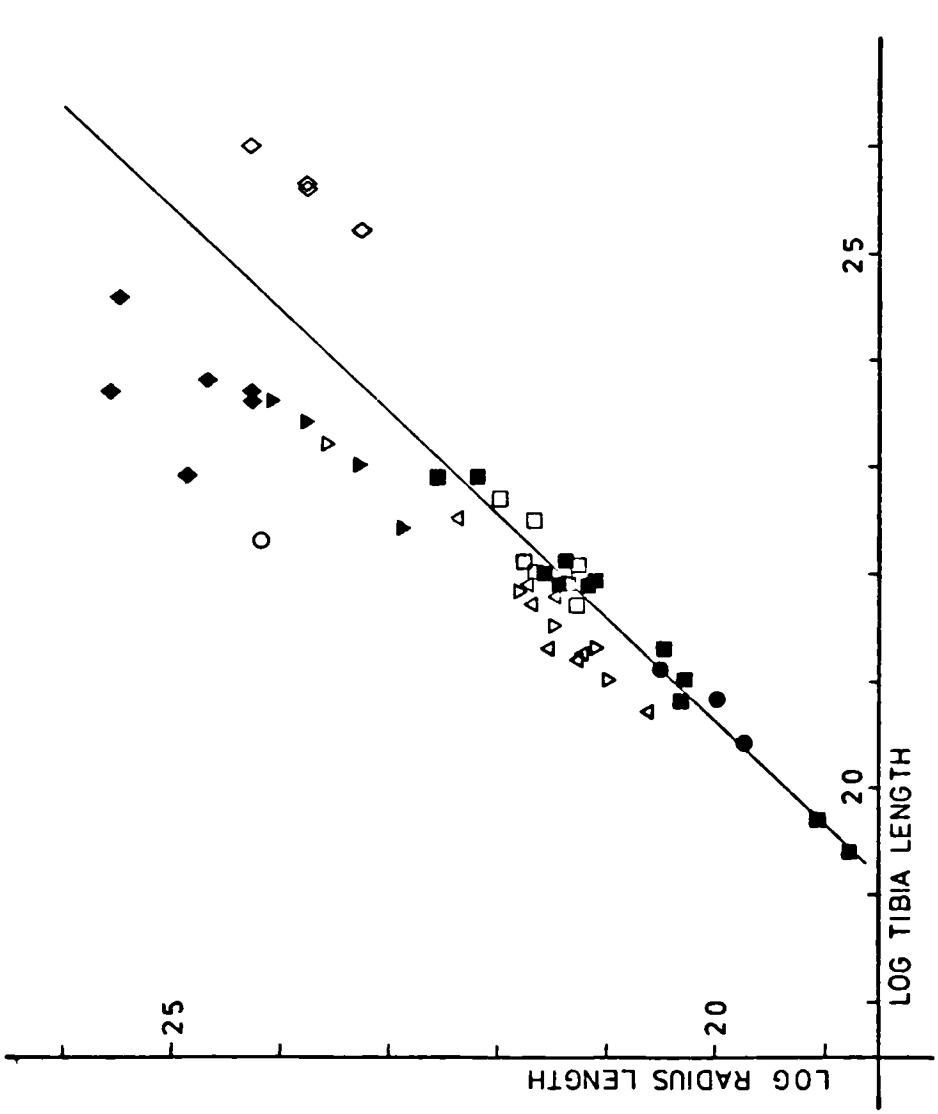

Fig. V.11. The relationship between the length of the tibia and the length of the radius.

Table V.12.

X = LOG RADIUS LENGTH Y = LOG TIBIA LENGTH

	GROUP 1
PRINCIPAL AXIS	.97 (.89 - 1.06)
REDUCED MAJOR AXIS	.97
LEAST SQUARES Y.X	Y = .16+.95X
SLOPE & 95% C.L.	.95 ± .12
INTERCEPT & 95% C.L.	.16 ± .25
LEAST SQUARES X.Y	X = -.09+1.02Y
SLOPE & 95% C.L.	1.02 ± .10
INTERCEPT & 95% C.L.	-.09 ± .22
CORRELATION COEFFICIENT	.984
COEF. OF DETERMINATION	.968
UNEXPLAINED VARIANCE Y.X	.00048
UNEXPLAINED VARIANCE X.Y	.00034
MEAN X	2.19
MEAN Y	2.18
SAMPLE SIZE	17

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

reflect the discussion in the previous sections.

1. The position of Homo sapiens is primarily the result of its relatively short radius in relation to its body weight.
2. The positions of Pan, Gorilla and Pongo are primarily the result of their relatively short tibias in relation to their body weights. The position of Pongo is accentuated by its relatively long radius in relation to its body weight.
3. The position of Papio anubis results from its relatively long radius in relation to its body weight.
4. The position of Hylobates results from its marginally long tibia and extremely long radius in relation to its body weight.

V. 13. The Relationship Between Body Weight and the Length of the Forelimb.

Fig. V. 12 illustrates the relationship between body weight and the length of the forelimb in the Group 1 and Group 11 primates. The principal axis for the combined Group 1 and Group 11 sample is isometric (Table V. 13). This relationship between body weight and the length of the forelimb is different from the relationship between body weight and length of the humerus for the combined sample. In the humerus length relationship the principal axis for the combined sample is positive (Section V. 7). The discrepancy between these two comparisons results from the relationship between body weight and the length of the radius in the Group 11 primates. The short radius in the majority of these primates results in a relatively short total forelimb length. The effect on this relationship between body weight and the total forelimb length is to produce a lower principal axis for the combined sample than observed in the relationship between body weight and the length of the humerus, i.e. an isometric principal axis rather than a positive principal axis. The consistency of the relationship between body weight and the length of the forelimb in the Group 1 and Group 11 primates is, therefore, only superficial.

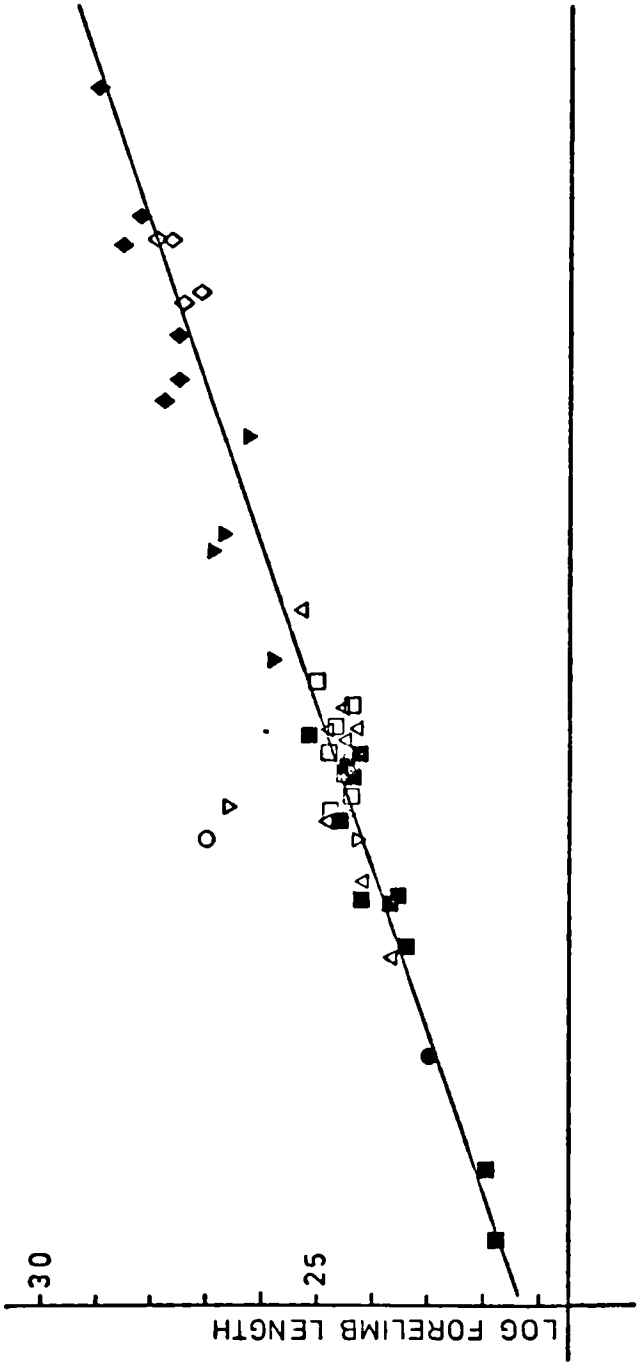

Fig. V.12. The relationship between body weight and the length of the forelimb.

Table V.13.

X = LOG BODY WEIGHT Y = LOG FOPELIMB LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.33 (.29 - .38)	.26 (.19 - .34)	.35 (.32 - .37)
REDUCED MAJOR AXIS	.34	.29	.35
LEAST SQUARES Y.X	Y = 1.19+.33X	Y = 1.54+.26X	Y = 1.13+.34X
SLOPE & 95% C.L.	.33 ± .05	.26 ± .09	.34 ± .03
INTERCEPT & 95% C.L.	1.19 ± .19	1.54 ± .43	1.13 ± .11
LEAST SQUARES X.Y	X = -3.11+2.84Y	X = -3.80+3.08Y	X = -2.98+2.78Y
SLOPE & 95% C.L.	2.84 ± .44	3.08 ± 1.09	2.78 ± .22
INTERCEPT & 95% C.L.	-3.11 ± 1.07	-3.80 ± 2.99	-2.98 ± .57
CORRELATION COEFFICIENT	.965	.895	.979
COEF. OF DETERMINATION	.932	.800	.959
UNEXPLAINED VARIANCE Y.X	.0007	.0015	.0015
UNEXPLAINED VARIANCE X.Y	.0060	.0175	.0122
MEAN X	3.75	4.71	4.14
MEAN Y	2.42	2.76	2.56
SAMPLE SIZE	16	12	31

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

It masks the significant non-allometric proportional differences in the forelimb of these primates. It is suggested that in cases other than the extreme forelimb elongation of Hylobates, the relationship between body weight and bone or limb lengths are not, in themselves, sufficient indicators of allometric relationships. In order to assess the biological significance of such allometric relationships it is necessary to consider the relationship between the two bones comprising the limbs, as well as the relationship between body weight and the lengths of individual bones and body weight and the total forelimb length.

V. 14. The Relationship Between the Length of the Forelimb and the Length of the Hindlimb

Fig. V. 13 illustrates the relationship between the length of the forelimb and the length of the hindlimb in the Group 1 and Group 11 primates. The principal axis for the Group 1 primates is isometric (Table V. 14). Therefore, in spite of the different allometric relationships between the individual bones of the limb, the forelimb and hindlimb increase at an approximately equal rate throughout the size range of these primates. Because the least squares intercept is significantly different from zero (Table V. 14) the hindlimb maintains an absolutely greater length throughout the size range.

All of the Group 11 primates are significantly different from the Group 1 trend.

1. Homo sapiens is indistinguishable from the Group 1 trend in the length of the hindlimb in relation to body weight and in the length of the humerus in relation to body weight. The significantly longer hindlimb in relation to the forelimb in this comparison is primarily due to its short radius.
2. Papio anubis is indistinguishable from the Group 1 trend in the length of its hindlimb in relation to body weight. Its position in this comparison is due to a long forelimb in relation to its body weight.

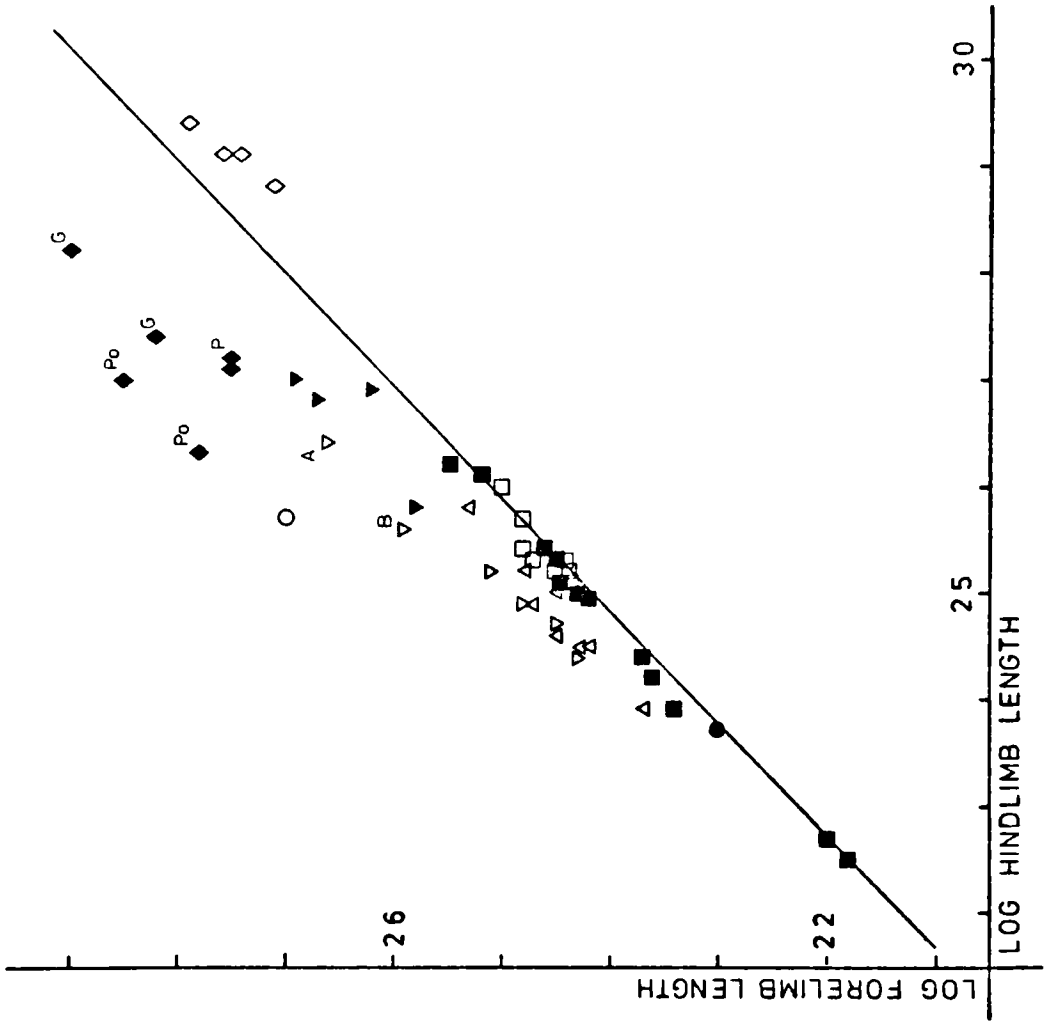

Fig. V.13. The relationship between the length of the forelimb and the length of the hindlimb.

Table V.14.

X = LOG HINDLIMB LENGTH Y = LOG FORELIMB LENGTH

	GROUP 1
PRINCIPAL AXIS	.96 (.91 - 1.01)
REDUCED MAJOR AXIS	.96
LEAST SQUARES Y.X	Y = .04+.95X
SLOPE & 95% C.L.	.95 ± .05
INTERCEPT & 95% C.L.	.04 ± .14
LEAST SQUARES X.Y	X = -.02+1.04Y
SLOPE & 95% C.L.	1.04 ± .06
INTERCEPT & 95% C.L.	-.02 ± .14
CORRELATION COEFFICIENT	.995
COEF. OF DETERMINATION	.989
UNEXPLAINED VARIANCE Y.X	.00011
UNEXPLAINED VARIANCE X.Y	.00012
MEAN X	2.50
MEAN Y	2.42
SAMPLE SIZE	17

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

3. Pan, Gorilla and Pongo are characterised by a short hindlimb in relation to their body weights. Their positions in this comparison primarily reflect this feature.
4. Hylobates has a significantly long forelimb, as well as hindlimb for its body weight. Its position in this comparison reflects a combination of these two factors.

V. 15. The Relationship Between Body Weight and the Intermembral Index

Fig. V. 14 illustrates the relationship between body weight and the intermembral index in the Group 1 and Group 11 primates. The lack of a significant correlation between body weight and the intermembral index in the Group 1 primates (Table V. 1) reflects the isometric increase of the length of the forelimb and the length of the hindlimb in relation to body weight and in relation to each other. The positions of the Group 1 primates in Fig. V. 14 illustrate the combined effects of the previously discussed factors relevant to limb length.

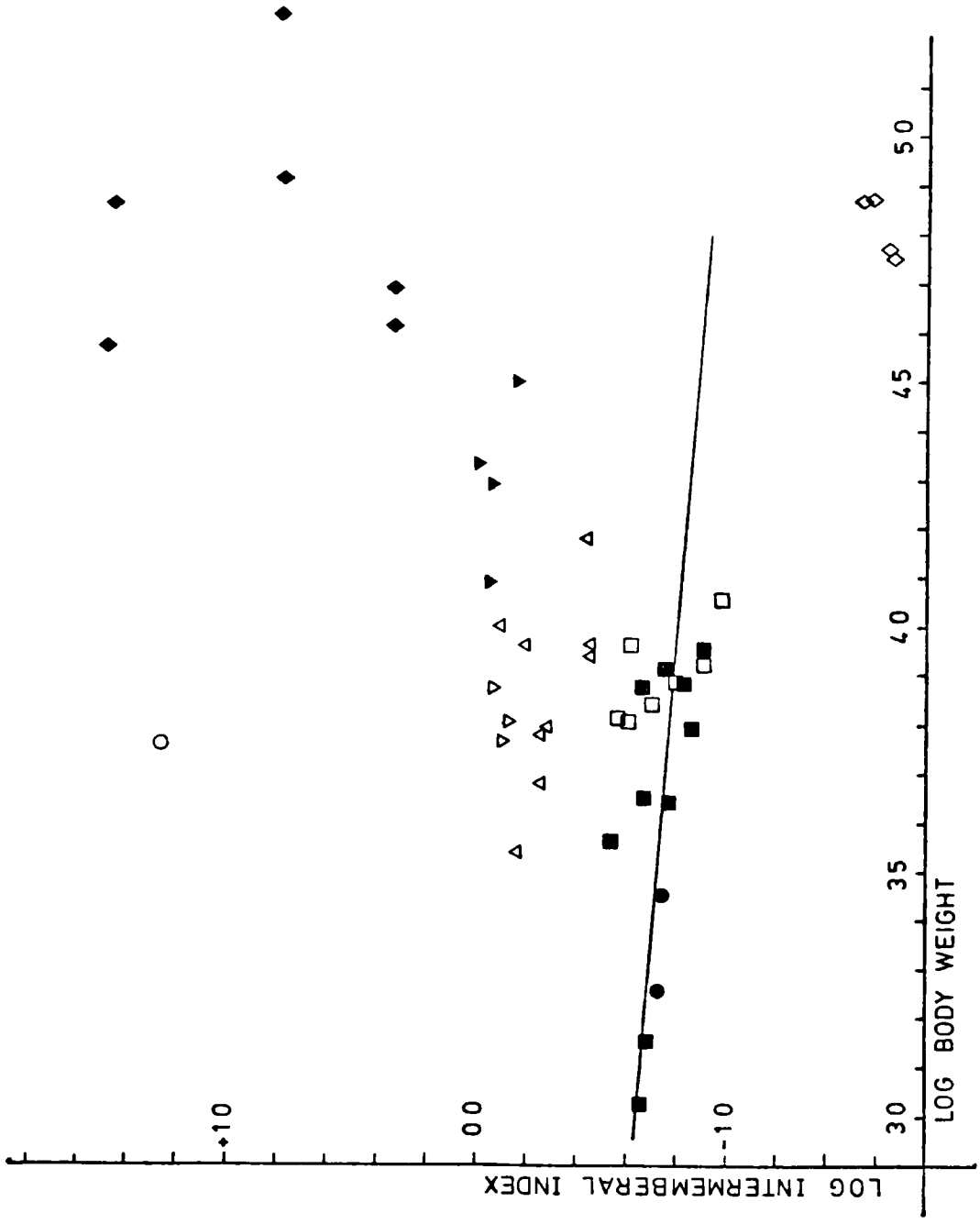

Fig. V.14. The relationship between body weight and the intermembral index.

Table V.15.

X = LOG BODY WEIGHT Y = LOG INTERMEMBRAL INDEX

	GROUP 1
PRINCIPAL AXIS	-.02 (-.04 - .00)
REDUCED MAJOR AXIS	.04
LEAST SQUARES Y.X	Y = -.01-.02X
SLOPE & 95% C.L.	-.02 ± .02
INTERCEPT & 95% C.L.	-.01 ± .08
LEAST SQUARES X.Y	X = 2.97-10.36Y
SLOPE & 95% C.L.	-10.36 ± 12.90
INTERCEPT & 95% C.L.	2.97 ± 1.04
CORRELATION COEFFICIENT	-.417
COEF. OF DETERMINATION	.174
UNEXPLAINED VARIANCE Y.X	.00012
UNEXPLAINED VARIANCE X.Y	.0723
MEAN X	3.75
MEAN Y	-.076
SAMPLE SIZE	16

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

VI. The Allometry of the Cross Section of the Long Bones in the Higher Primates

VI. 1. Introduction

The cross section of a bone traditionally has been characterised by one or a combination of its external measurements, i.e. by its circumference, average diameter, sagittal diameter or transverse diameter. These measurements are not entirely satisfactory. Chapter IV has shown that although these measurements account for the maprity of the variance of the strength measurements (the idealised section modulus and the idealised area) they do not all relate to these measurements in an isometric fashion. In addition, the same external measurements taken on the humerus and on the femur relate to the idealised area or to the idealised section modulus of the respective bones in different fashion. Therefore, there is no consistency in the manner in which the external measurements relate to the idealised strength measurements. This inconsistency results from variation in the cortical thickness and in the shape of the cross section.

This chaper will examine the allometry of the external measurements of the bone cross section, the cortical thickness and the idealised strength measurements.

VI. 2. The Relationship Between the Sagittal Diameter of the Femur and Body Weight

Fig. VI.1 illustrates the relationship between the body weight and the femur sagittal diameter in the Group I and Group II primates. The principal axis is positive (Table VI.1). Fig. VI.1 clearly gives the impression that the majority of the variance left unexplained by body weight is found among the Group II primates. There is a significantly greater amount of the variance explained by this relationship in the Group I primates than in the Group II primates, although the two samples cannot be distinguished on the basis of either their least squares slopes or their intercepts. Tested against the Group I trend, the two obvious outlying species are Homo and Pongo. Homo has a sagittal diameter greater than would be expected for its body weight and Pongo has a sagittal diameter smaller than would be

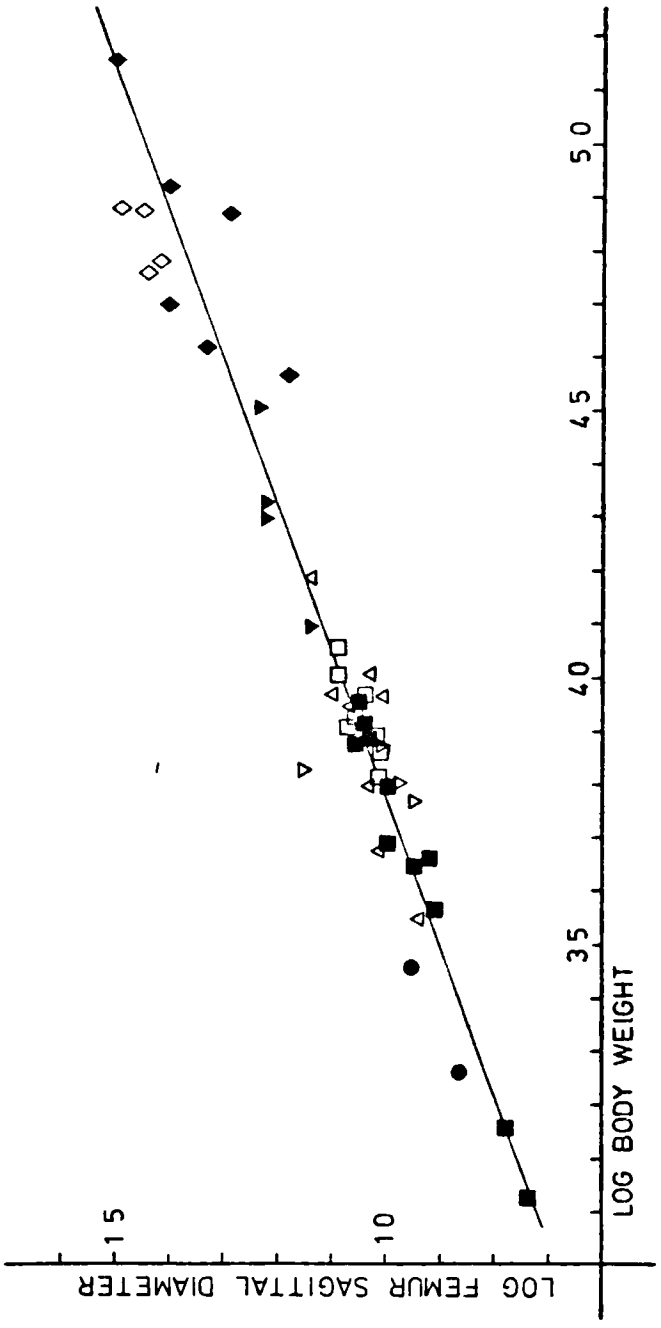

Fig. VI.1. The relationship between body weight and the sagittal diameter of the femur.

Table VI.1.

X = LOG BODY WEIGHT Y = LOG FEMUR SAGITTAL DIAMETER

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.35 (.31 - .38)	.39 (.26 - .53)	.37 (.35 - .40)
REDUCED MAJOR AXIS	.55	.43	.38
LEAST SQUARES Y.X	Y = -.30+.34X	Y = -.41+.37X	Y = -.40+.37X
SLOPE & 95% C.L.	.34 ± .04	.37 ± .16	.37 ± .03
INTERCEPT & 95% C.L.	-.30 ± .15	-.41 ± .74	-.40 ± .12
LEAST SQUARES X.Y	X = 1.02+2.76Y	X = 2.04+1.98Y	X = 1.20+2.58Y
SLOPE & 95% C.L.	2.76 ± .32	1.98 ± .83	2.58 ± .21
INTERCEPT & 95% C.L.	1.02 ± .12	2.04 ± 1.13	1.20 ± .24
CORRELATION COEFFICIENT	.974	.859	.978
COEF. OF DETERMINATION	.948	.738	.956
UNEXPLAINED VARIANCE Y.X	.00048	.0044	.0019
UNEXPLAINED VARIANCE X.Y	.0039	.0232	.0131
MEAN X	3.76	4.71	4.11
MEAN Y	.99	1.35	1.13
SAMPLE SIZE	20	12	32

GROUP 1 — COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 — PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 — GROUP 1 AND GROUP 2

expected. It is, therefore, reasonable to conclude that the femur sagittal diameter is isometric with body weight within the Group I and Group II primates, with the exception of Homo and Pongo.

VI. 3. The Relationship Between the Transverse Diameter of the Femur and Body Weight

Fig. VI.2 illustrates the relationship between body weight and femur transverse diameter. The principal axis for the combined Group I and Group II sample is positive. Table VI. 2 indicates that the Group I primates cannot be distinguished from the Group II primates on the basis of the least squares slopes, intercepts or on the amount of variance explained by the relationship of the two variables. Therefore, it is possible to conclude that the femur transverse diameter has a constant relationship with body weight across the entire Group I and Group II sample. Based on the Group I sample, however, Gorilla and Pan have femur transverse diameters which are statistically larger than expected. Therefore, it is not entirely clear whether or not the trend is homogenous.

VI. 4. The Relationship Between the Transverse Diameter of the Femur and the Sagittal Diameter of the Femur

When the sagittal diameter of the femur is plotted against the transverse diameter of the femur (Fig. VI. 3) the principal axis for the Group I primates is not significantly different from isometry (Table VI. 3). Based on the projection of this trend Homo sapiens is statistically different from the Group I primates in having a larger sagittal diameter than expected in relation to its femur transverse diameter. Gorilla and Pongo are also different in having a larger transverse diameter than expected based on their sagittal diameters. From Figs. VI.1 and VI. 2 and Tables VI.1 and VI. 2, the larger femur sagittal diameter compared to femur transverse diameter in Homo sapiens results from a larger than expected sagittal diameter for its body weight. The larger than expected transverse diameter in Pongo results from a much smaller than expected

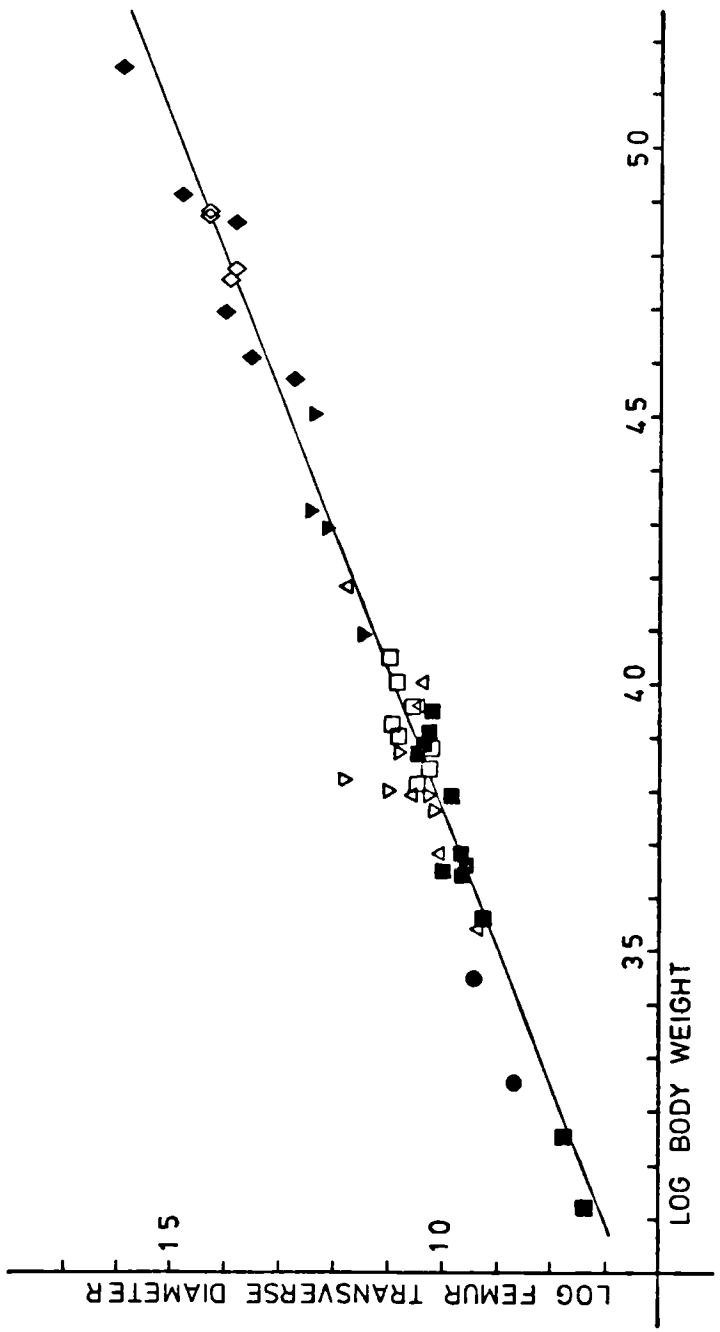

Fig. VI.2. The relationship between body weight and the transverse diameter of the femur.

Table VI.2.

X = LOG BODY WEIGHT Y = LOG FEMUR TRANSVERSE DIAMETER

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.35 (.32 - .39)	.40 (.34 - .47)	.39 (.38 - .41)
REDUCED MAJOR AXIS	.36	.41	.40
LEAST SQUARES Y.X	Y = -.48+.40X	Y = -.48+.40X	Y = -.47+.39X
SLOPE & 95% C.L.	.40 ± .06	.40 ± .08	.39 ± .02
INTERCEPT & 95% C.L.	-.48 ± .28	-.48 ± .37	-.47 ± .08
LEAST SQUARES X.Y	X = 1.05+2.71Y	X = 1.47+2.34Y	X = 1.25+2.50Y
SLOPE & 95% C.L.	2.71 ± .32	2.34 ± .46	2.50 ± .12
INTERCEPT & 95% C.L.	1.05 ± .32	1.47 ± .64	1.25 ± .14
CORRELATION COEFFICIENT	.972	.963	.992
COEF. OF DETERMINATION	.945	.927	.984
UNEXPLAINED VARIANCE Y.X	.00053	.0011	.00078
UNEXPLAINED VARIANCE X.Y	.0041	.0064	.0050
MEAN X	3.76	4.71	4.11
MEAN Y	1.00	1.38	1.15
SAMPLE SIZE	20	12	32

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

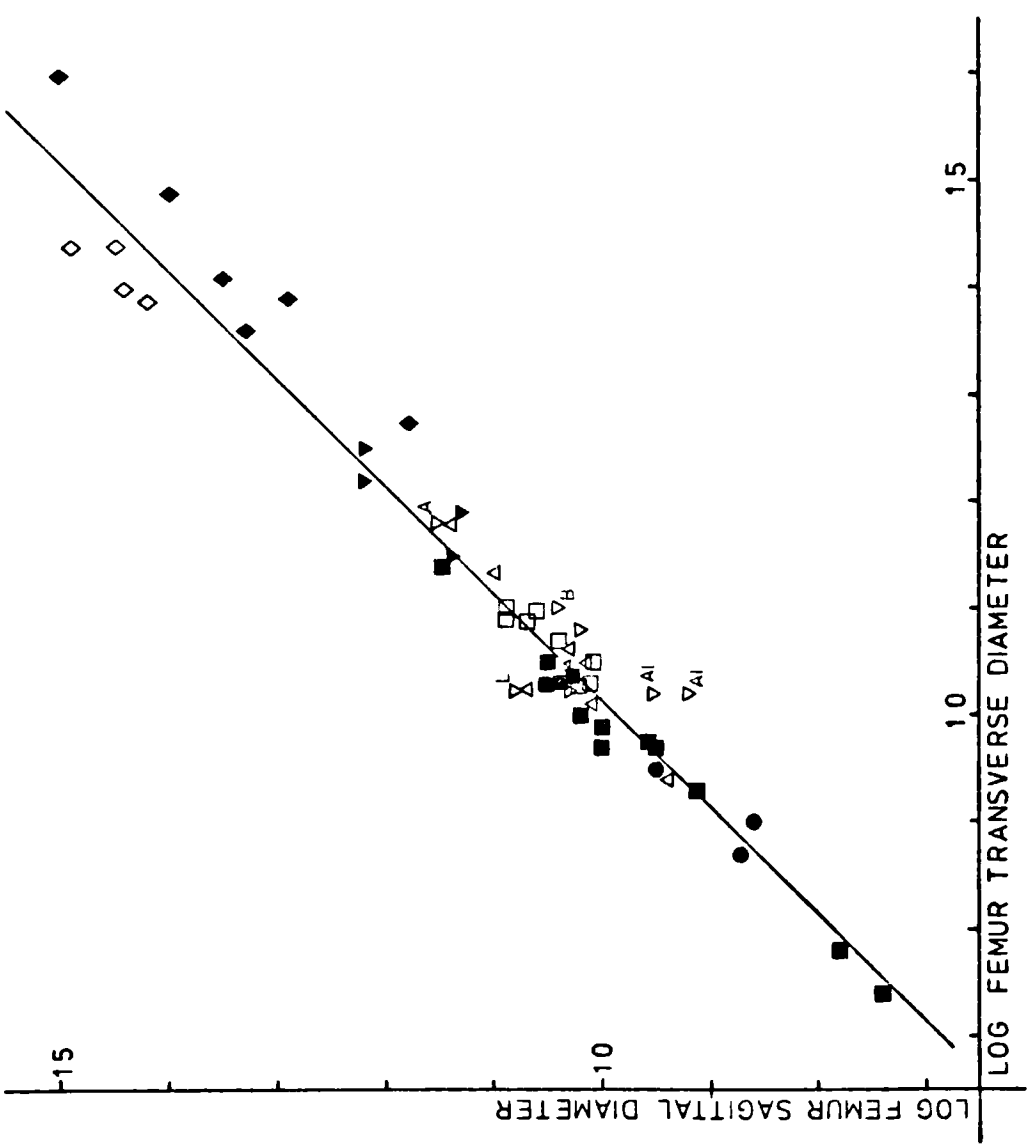

Fig. VI.3. The relationship between the sagittal diameter of the femur and the transverse diameter of the femur.

Table VI.3.

X = LOG FEMUR TRANSVERSE DIAMETER Y = LOG FEMUR SAGITTAL DIAMETER

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.98 (.90 - 1.08)	.86 (.61 - 1.21)	.95 (.89 - 1.02)
REDUCED MAJOR AXIS	.98	.88	.96
LEAST SQUARES Y.X	Y = .03+.96X	Y = .32+.76X	Y = .05+.94X
SLOPE & 95% C.L.	.96 ± .10	.76 ± .32	.94 ± .07
INTERCEPT & 95% C.L.	.03 ± .10	.32 ± .44	.05 ± .08
LEAST SQUARES X.Y	X = .01+1.00Y	X = .05+.97Y	X = -.02+1.03Y
SLOPE & 95% C.L.	1.00 ± .11	.97 ± .41	1.03 ± .07
INTERCEPT & 95% C.L.	.01 ± .11	.05 ± .56	-.02 ± .08
CORRELATION COFFFICIENT	.978	.858	.983
COEF. OF DETERMINATION	.957	.737	.966
UNEXPLAINED VARIANCE Y.X	.0004	.0037	.0015
UNEXPLAINED VARIANCE X.Y	.0004	.0047	.0016
MEAN X	1.00	1.38	1.15
MEAN Y	.993	1.36	1.13
SAMPLE SIZE	20	12	32

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

sagittal diameter for its body weight, while the transverse diameter meets the Group 1 expectations. The larger than expected transverse diameter for body weight in Gorilla results from a larger than expected transverse diameter for its body weight with the expected sagittal diameter based on the Group 1 trend.

Therefore, returning to Fig. VI.2 and the relationship between body weight and femur transverse diameter, it is reasonable to conclude that, in spite of the statistical identity between the Group 1 primates and the Group II primates, the relationship between body weight and femur transverse diameter is at least different for Pan and Gorilla, resulting in their outlying position in the comparison between femur transverse diameter and femur sagittal diameter. Therefore, there is a significant change in the shape of the cross section of the femur in some of the primates making up the Group II sample which cannot be accounted for by increase in body weight alone.

VI. 5. The Relationship Between the Transverse Diameter of the Humerus and Body Weight

Fig. VI.4 illustrates the relationship between body weight and the humerus transverse diameter. The principal axis is not significantly different from isometry (Table VI.4).

When the entire sample is divided into the Group 1 primates and the Group II primates there is no significant difference in the least squares slopes or intercepts between these two samples. There is also no significant difference in the amount of variance of the humerus transverse diameter left unexplained by its relationship to body weight. Therefore, there is no statistical reason to suggest that there are two separate trends within the combined Group 1 and Group II sample, or to suggest that one sample is more variable than the other. It is, therefore, reasonable to conclude that the humerus transverse diameter stands in a constant isometric relationship with body weight across the entire sample.

Within the Group 1 sample there is an interesting clustering

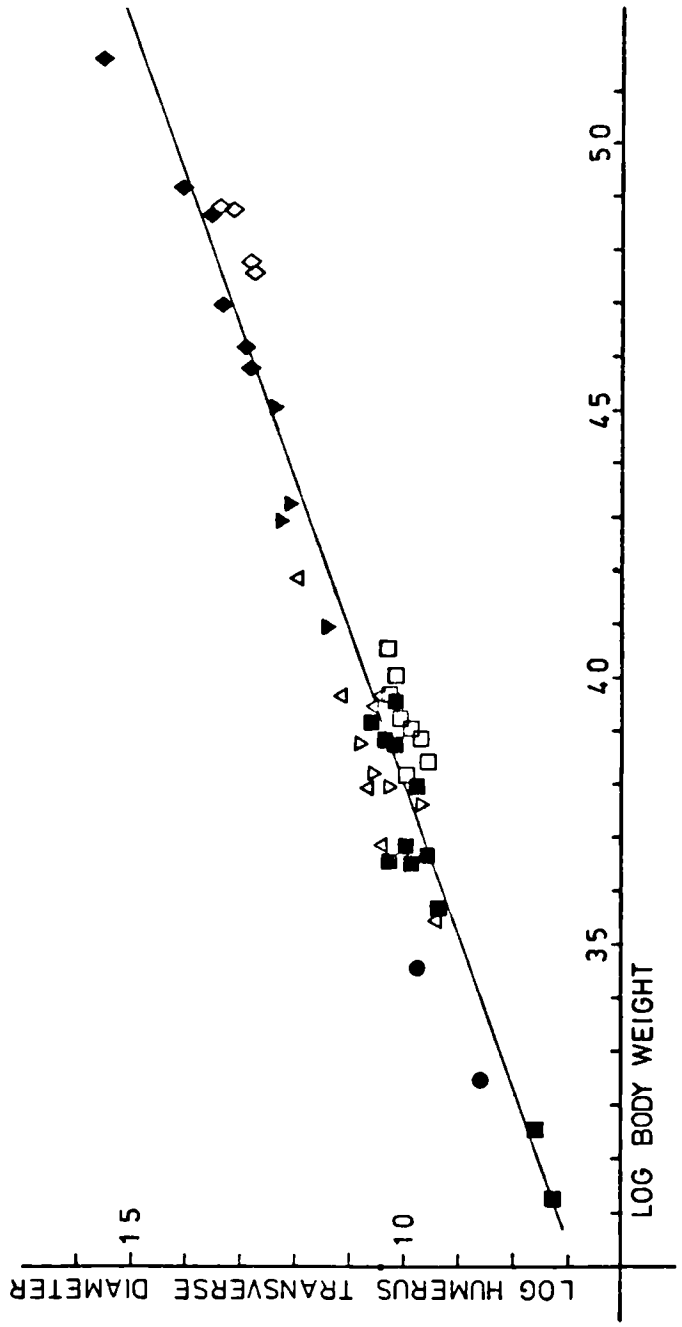

Fig. VI.4. The relationship between body weight and the transverse diameter of the humerus.

Table VI.4.

X = LOG BODY WEIGHT Y = LOG HUMERUS TRANSVERSE DIAMETER

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.29 (.23 - .35)	.35 (.26 - .44)	.35 (.33 - .38)
REDUCED MAJOR AXIS	.32	.37	.36
LEAST SQUARES Y.X	Y = -.10+.29X	Y = -.03+.29X	Y = -.33+.35X
SLOPE & 95% C.L.	.29 ± .07	.29 ± .11	.35 ± .03
INTERCEPT & 95% C.L.	-.10 ± .25	-.27 ± .51	-.33 ± .12
LEAST SQUARES X.Y	X = .96+2.87Y	X = 1.46+2.45Y	X = 1.09+2.73Y
SLOPE & 95% C.L.	2.87 ± .66	2.45 ± .79	2.73 ± .22
INTERCEPT & 95% C.L.	.96 ± .64	1.46 ± 1.05	1.09 ± .25
CORRELATION COEFFICIENT	.907	.909	.977
COEF. OF DETERMINATION	.823	.827	.955
UNEXPLAINED VARIANCE Y.X	.0013	.0021	.0017
UNEXPLAINED VARIANCE X.Y	.0132	.0152	.0134
MEAN X	3.76	4.71	4.11
MEAN Y	.98	1.32	1.11
SAMPLE SIZE	20	12	32

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

of species in relation to the principal axis. With the exception of Cercopithecus talapoin all of the Group 1 cercopithecines lie above the principal axis and all of the colobines, as well as Presbytis, lie below the principal axis. Therefore, these Group 1 cercopithecines have a slightly larger than predicted humerus transverse diameter for their body weight, while the colobines and Presbytis have smaller than expected humerus transverse diameters.

VI. 6. The Relationship Between the Sagittal Diameter of the Humerus and Body Weight

Fig. VI. 5 illustrates the relationship between body weight and the humerus sagittal diameter. The principal axis for the combined Group 1 and Group II sample is positive, while the principal axes for the Group 1 and Group II sample are not significantly different from isometry (Table VI. 5). However, the Group 1 sample does not differ significantly from the Group II sample in either the least squares slopes or intercepts. Therefore, these two samples cannot statistically be considered to have come from separate populations. The positive principal axis for the combined sample is, therefore, statistically the best characterisation of the trend. Table VI. 5 shows, however, that the two subsamples differ significantly in the magnitude of the variance of the humerus sagittal diameter explained by its relationship with body weight. The Group II sample is significantly more variable. In addition, when the primates included in the Group II sample are tested individually for inclusion within the Group 1 trend, all but Homo are significantly different. These Group II primates possess a larger humerus sagittal diameter than expected for their body weights on the basis of this trend. The relationship between the humerus sagittal diameter and body weight is, therefore, ambiguous.

VI. 7. The Relationship Between the Sagittal Diameter of the Humerus and the Transverse Diameter of the Humerus

When the sagittal diameter of the humerus is plotted against the transverse diameter of the humerus (Fig. VI. 6) the

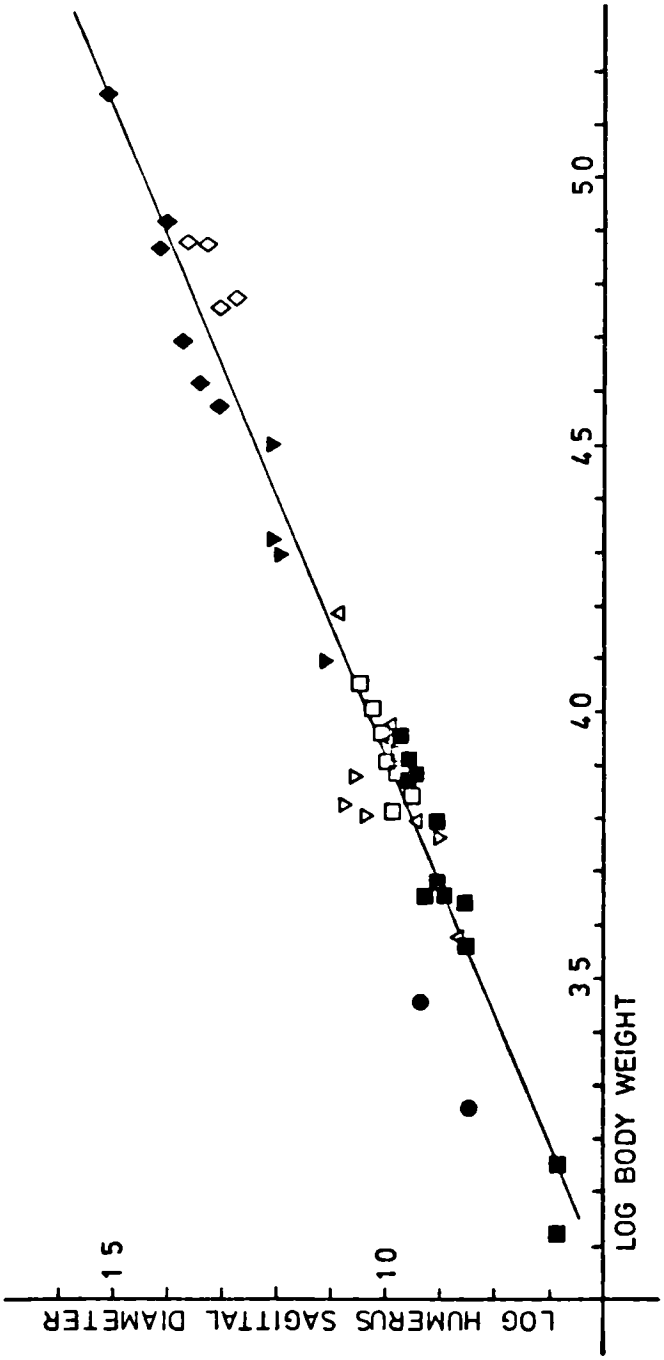

Fig. VI.5. The relationship between body weight and the sagittal diameter of the humerus.

Table VI.5.

X = LOG BODY WEIGHT Y = LOG HUMERUS SAGITTAL DIAMETER

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.35 (.31 - .39)	.34 (.26 - .43)	.41 (.38 - .43)
REDUCED MAJOR AXIS	.36	.37	.41
LEAST SQUARES Y.X	Y = -.38+.35X	Y = -.28+.34X	Y = -.58+.40X
SLOPE & 95% C.L.	.35 ± .04	.34 ± .10	.40 ± .03
INTERCEPT & 95% C.L.	-.38 ± .16	-.25 ± .49	-.58 ± .10
LEAST SQUARES X.Y	X = 1.24+2.71Y	X = 1.38+2.50Y	X = 1.50+2.41Y
SLOPE & 95% C.L.	2.71 ± .33	2.50 ± .77	2.41 ± .15
INTERCEPT & 95% C.L.	1.24 ± .31	1.38 ± 1.03	1.50 ± .16
CORRELATION COEFFICIENT	.972	.916	.987
COEF. OF DETERMINATION	.944	.838	.974
UNEXPLAINED VARIANCE Y.X	.0005	.0019	.0013
UNEXPLAINED VARIANCE X.Y	.0042	.0142	.0079
MEAN X	3.76	4.71	4.11
MEAN Y	.93	1.33	1.08
SAMPLE SIZE	20	12	32

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

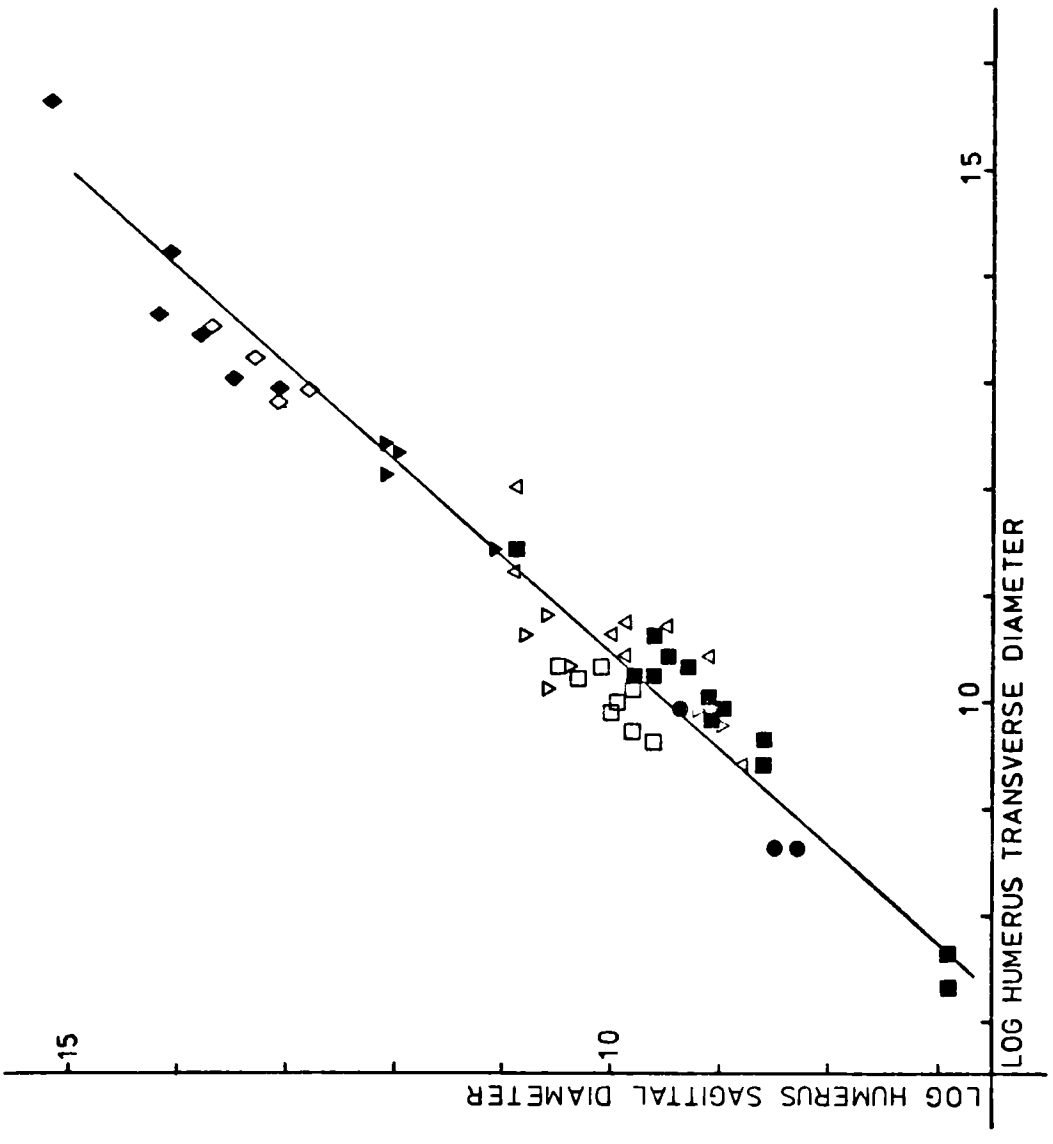

Fig. VI.6. The relationship between the transverse diameter of the humerus and the sagittal diameter of the humerus.

Table VI.6.

X = LOG HUMERUS TRANSVERSE DIAMETER Y = LOG HUMERUS SAGITTAL DIAMETER

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	1.15 (.92 - 1.44)	.99 (.83 - 1.17)	1.15 (1.07 - 1.22)
REDUCED MAJOR AXIS	1.13	.99	1.14
LEAST SQUARES Y.X	Y = -.11+1.01X	Y = .08+.95X	Y = -.16+1.12X
SLOPE & 95% C.L.	1.01 ± .25	.95 ± .20	1.12 ± .08
INTERCEPT & 95% C.L.	-.06 ± .25	.08 ± .26	-.16 ± .09
LEAST SQUARES X.Y	X = .25+.79Y	X = .03+.97Y	X = .18+.85Y
SLOPE & 95% C.L.	.79 ± .20	.97 ± .21	.85 ± .06
INTERCEPT & 95% C.L.	.25 ± .18	.03 ± .09	.18 ± .07
CORRELATION COEFFICIENT	.892	.959	.983
COEF. OF DETERMINATION	.796	.919	.965
UNEXPLAINED VARIANCE Y.X	.00197	.00096	.0017
UNEXPLAINED VARIANCE X.Y	.0015	.00098	.0013
MEAN X	.98	1.32	1.11
MEAN Y	.93	1.33	1.08
SAMPLE SIZE	20	12	32

GROUP 1 — COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 — PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 — GROUP 1 AND GROUP 2

principal axis for the combined Group I and Group II sample is significantly positive.

The Group I sample and the Group II sample are not significantly different from each other or from isometry. The Group I sample and the Group II sample also cannot be distinguished on the basis of their least squares slopes or intercepts and, therefore, cannot be statistically differentiated. Table VI.6 indicates, however, that a greater magnitude of the variance is explained by the relationship in the Group II primates than in the Group I primates. Within the Group I primates there is again a visual distinction between the Group I cercopithecines and the colobines and Presbytis. The Group I cercopithecines have a larger than expected humerus transverse diameter for their humerus sagittal diameters and for their body weights. This would most likely be the result of the strong development of the deltoid crest in these species, which lies immediately above the midpoint of the humerus shaft. It is also interesting that the Group I primates are most variable in the relationship between body weights and humerus transverse diameter, while Group II primates are most variable in the relationship between humerus sagittal diameter and body weight.

VI. 8. The Shape of the Cross Section of the Femur and the Shape of the Cross Section of the Humerus

In summary, the allometry of the shape of the midshaft cross section of both the humerus and the femur indicate that weight is not a constant correlate of cross section shape across the sample. In the femur, Pan and Gorilla are significantly different from the remaining primates in having a transversely ovoid cross section. Homo is also significantly different in having a larger sagittal diameter for its femur transverse diameter. In absolute magnitude of the cross section the femur sagittal diameter is larger in Homo and smaller in Pongo. The femur transverse diameter is larger in both Pan and Gorilla. Therefore, both size and shape of the cross section do not relate to body weight consistently across the sample.

The same inconsistency with body weight is also apparent in the humerus cross section. In the comparison between the sagittal diameter of the humerus and the transverse diameter of the humerus the Group I primates are considerably more variable than are the Group II primates. This situation results from variation in the relationship between body weights and the humerus transverse diameter. The cercopithecines within the Group I primates are characterised by a significantly larger transverse diameter for their body weights and sagittal diameters than are the colobines and Presbytis. In the absolute magnitude of the sagittal diameter and the transverse diameter, Pan, Gorilla and Pongo are all characterised by significantly larger diameters than is Homo sapiens.

VI. 9. The Relationship Between Body Weight and the Circumference of the Femur and Between Body Weight and the Circumference of the Humerus

Fig. VI. 7 and Fig. VI. 8 illustrate the relationships between body weight and the circumference of the femur and between body weight and the circumference of the humerus. Both of these relationships show the same pattern as do the relationships between body weight and the idealised section modulus and between body weight and the idealised cross section area for the individual bones (Figs. VI. 13 & VI. 14). The Group II primates are significantly more variable than is the Group I sample (Tables VI. 7 and VI. 8). In the relationship between body weight and femur circumference, Pongo deviates from the remaining Group II primates in the direction of a smaller femur circumference for its body weight. The remaining Group II primates lie above the extension of the Group I principal axis. When these species are tested for inclusion within the Group I trend, only Papio anubis (female), Gorilla (female) and Homo sapiens (caucasian, male and female) clearly belong to the trend. Papio anubis (male), Pongo (female) and Homo sapiens (negro, male and female) are clearly different from the trend. The remaining primates are ambiguous in their affinities.

In the relationship between body weight and humerus

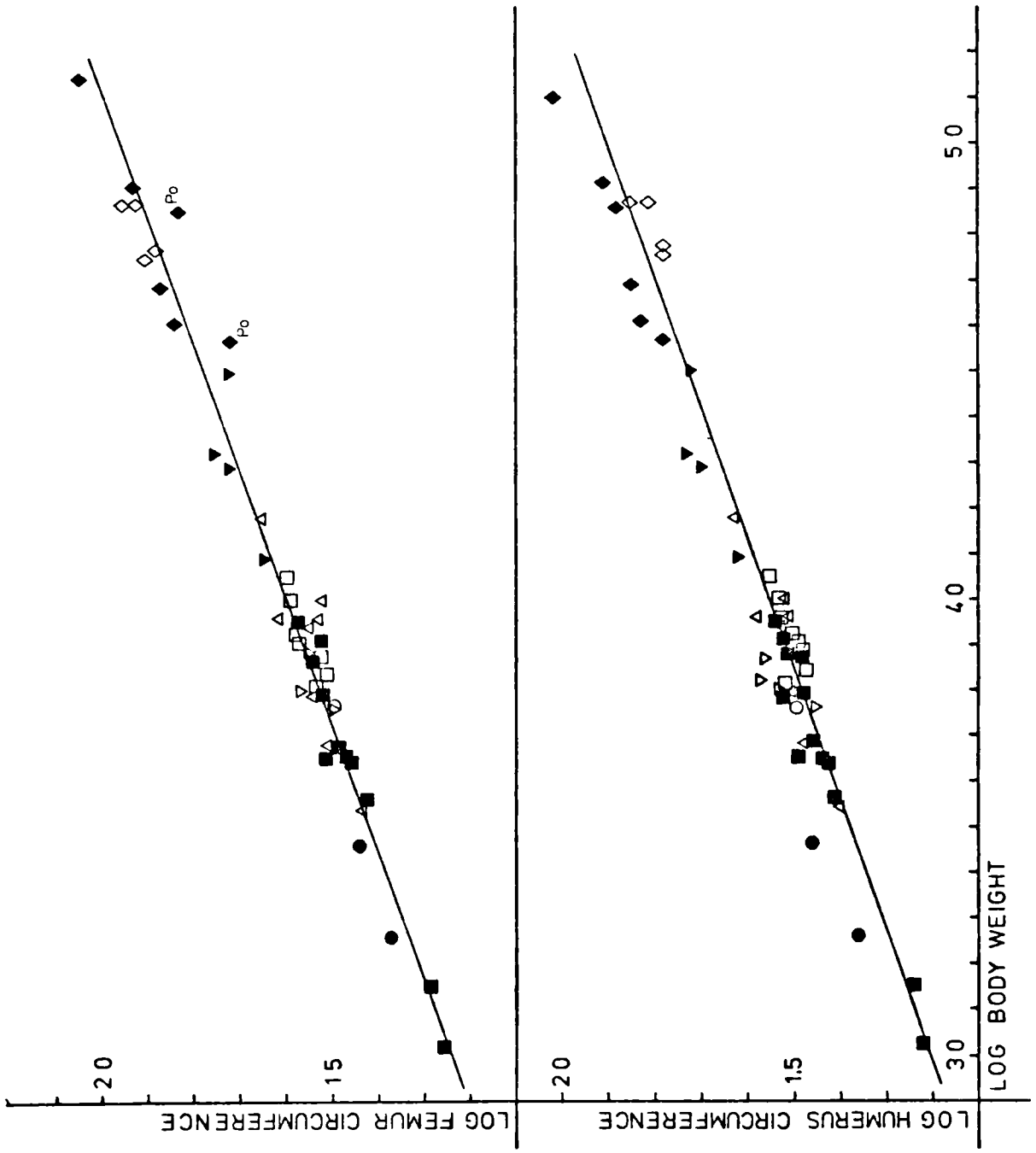

Fig. VI.7.
The relationship between body weight and the circumference of the femur.

Fig. VI.8.
The relationship between body weight and the circumference of the humerus.

Table VI.7.

X = LOG BODY WEIGHT Y = LOG FEMUR CIRCUMFERENCE

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.34 (.31 - .37)	.37 (.29 - .46)	.37 (.35 - .39)
REDUCED MAJOR AXIS	.34	.39	.37
LEAST SQUARES Y.X	Y = .24+.34X	Y = .16±.36X	Y = .12+.37X
SLOPE & 95% C.L.	.34 ± .03	.36 ± .11	.37 ± .02
INTERCEPT & 95% C.L.	.24 ± .12	.16 ± .50	.12 ± .08
LEAST SQUARES X.Y	X = -.56+2.86Y	X = .32+2.35Y	X = -.24+2.65Y
SLOPE & 95% C.L.	2.86 ± .26	2.35 ± .69	2.65 ± .14
INTERCEPT & 95% C.L.	-.56 ± .39	.32 ± 1.29	-.24 ± .24
CORRELATION COEFFICIENT	.984	.924	.989
COEF. OF DETERMINATION	.968	.853	.979
UNEXPLAINED VARIANCE Y.X	.00029	.0020	.0009
UNEXPLAINED VARIANCE X.Y	.0024	.0129	.0063
MEAN X	3.76	4.71	4.10
MEAN Y	1.51	1.87	1.64
SAMPLE SIZE	20	12	33

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

Table VI.8.

X = LOG BODY WEIGHT Y = LOG HUMERUS CIRCUMFERENCE

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.32 (.29 - .36)	.33 (.24 - .42)	.37 (.34 - .39)
REDUCED MAJOR AXIS	.33	.35	.37
LEAST SQUARES Y.X	Y = .26+.32X	Y = .32+.32X	Y = .10+.36X
SLOPE & 95% C.L.	.32 ± .04	.32 ± .11	.36 ± .02
INTERCEPT & 95% C.L.	.26 ± .15	.32 ± .51	.10 ± .10
LEAST SQUARES X.Y	X = -.52+2.93Y	X = .07+2.54Y	X = -.16+2.67Y
SLOPE & 95% C.L.	2.93 ± .37	2.54 ± .86	2.67 ± .17
INTERCEPT & 95% C.L.	-.52 ± .54	.07 ± 1.58	-.16 ± .27
CORRELATION COEFFICIENT	.969	.901	.986
COEF. OF DETERMINATION	.939	.812	.971
UNEXPLAINED VARIANCE Y.X	.0005	.0021	.0011
UNEXPLAINED VARIANCE X.Y	.0046	.0165	.0084
MEAN X	3.76	4.71	4.10
MEAN Y	1.46	1.82	1.59
SAMPLE SIZE	20	12	33

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

circumference Homo sapiens is the only member of the Group II sample which statistically belongs to the Group I trend, while the remaining species deviate in the direction of a larger humerus circumference for their body weights than would be expected on the basis of this trend. Therefore, as with the relation between body weight and femur circumference, there is a constant relationship between body weight and humerus circumference in the Group I sample and a more variable relationship in the Group II sample.

One difference in the relationship between body weight and femur circumference in the Group I sample in relation to the other femur cross section measurements is that the femur circumference is isometric with body weight, while both the idealised femur section modulus and the idealised femur area are significantly positively allometric (Figs. VI. 13 and VI. 16, Tables VI. 13 and VI. 16). This results from the positive relationship between cortical thickness and femur circumference (Section IV. 4) which produces a disproportionately larger idealised femur cross section area and idealised femur section modulus for the femur circumference as the femur circumference increases in size in the Group I sample.

The strength of the cross section as measured by the idealised femur section modulus and the idealised femur cross section area, therefore, increases more rapidly in relation to body weight than does the circumference of the femur.

VI. 10. The Relationship Between the Circumference of the Femur and the Circumference of the Humerus

Fig. VI. 9 illustrates the relationship between femur circumference and humerus circumference. The principal axis for the Group I sample is isometric, indicating that the femur circumference and the humerus circumference are increasing at an equal rate in relation to body size (Table VI. 9). When the primates in the Group II sample are tested against this trend, Pongo and Homo sapiens are the only clearly deviant primates. Pongo has a large humerus circumference for its

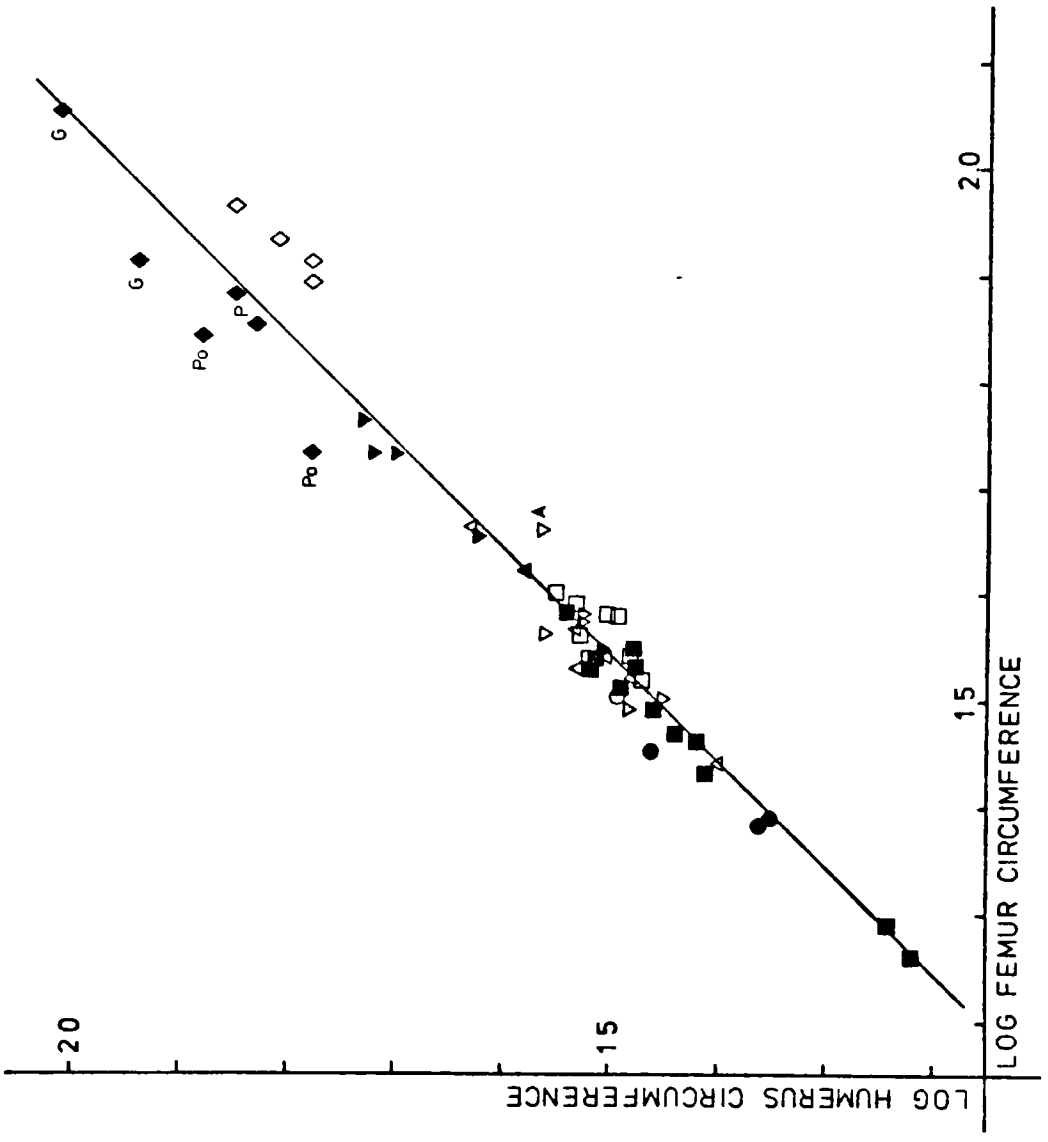

Fig. VI.9. The relationship between the circumference of the femur and the circumference of the humerus.

Table VI.9.

X = LOG FEMUR CIRCUMFERENCE Y = LOG HUMERUS CIRCUMFERENCE

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.97 (.88 - 1.06)	.89 (.60 - 1.29)	.99 (.92 - 1.06)
REDUCED MAJOR AXIS	.97	.90	.99
LEAST SQUARES Y.X	Y = .03+.95X	Y = .41+.75X	Y = -.04+.97X
SLOPE & 95% C.L.	.95 ± .10	.75 ± .35	.97 ± .07
INTERCEPT & 95% C.L.	.03 ± .15	.41 ± .65	-.04 ± .11
LEAST SQUARES X.Y	X = .04+1.01Y	X = .18+.93Y	X = .06+.99Y
SLOPE & 95% C.L.	1.01 ± .10	.93 ± .43	.99 ± .07
INTERCEPT & 95% C.L.	.04 ± .15	.18 ± .78	.06 ± .12
CORRELATION COEFFICIENT	.978	.835	.980
COEF. OF DETERMINATION	.956	.698	.961
UNEXPLAINED VARIANCE Y.X	.00039	.0033	.0015
UNEXPLAINED VARIANCE X.Y	.00041	.0041	.0016
MEAN X	1.52	1.87	1.64
MEAN Y	1.47	1.82	1.60
SAMPLE SIZE	21	12	33

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

femur circumference and Homo sapiens has a large femur circumference for its humerus circumference. Although Papio anubis, Pan and Gorilla are not statistically different from the Group 1 trend, they all lie slightly above the principal axis for this trend, indicating a large humerus circumference for their femur circumference. All of these species also fall above the Group 1 principal axis in the relationship between body weight and both femur circumference and humerus circumference (Figs. VI.7 and VI.8). Their position in the relationship between femur circumference and humerus circumference indicates that they have a larger humerus circumference in relation to body weight than they have a femur circumference in relation to body weight. Their identity with the Group 1 sample in this relationship is a reflection of the increase of both femur circumference and humerus circumference in relation to body weight and not necessarily a reflection of identity with the Group 1 sample in the relationship between both humerus circumference and femur circumference and body weight.

VI. 11. The Relationship Between Body Weight and the Average Midshaft Cortical Thickness of the Femur and Between Body Weight and the Average Midshaft Cortical Thickness of the Humerus

Cortical thickness is the variable in the analysis of the cross section measurements of the femur which accounts for the non-isometry of the external cross section measurements with the idealised femur cross section area and for the variable relationship of the external cross section measurements with the idealised femur section modulus (Section IV.4). It is significantly positively allometric with all of the external measurements in the femur cross section, while it is isometric with all of the external measurements of the humerus except for humerus transverse diameter, with which it is just significantly negatively allometric (Section IV.5). This suggests that cortical thickness relates to body weight in different fashions in the femur and in the humerus. This section will examine these relationships.

Fig. VI.10 illustrates the allometry of the average midshaft cortical thickness of the femur and Fig. VI.11 the allometry of the average midshaft cortical thickness of the humerus. The principal axis for the femur comparison is significantly different from the principal axis for the humerus comparison (Tables VI.10 and VI.11). Although both the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus are positively allometric in relation to body weight, the average midshaft cortical thickness of the femur is significantly more positive than is the average midshaft cortical thickness of the humerus. This relationship is also generally true when the two subsamples, the Group I primates and the Group II primates are analysed separately. The Group I sample and the Group II sample are characterised by higher principal axes in the comparisons between body weight and the average midshaft cortical thickness of the femur than in the comparison between body weight and the average midshaft cortical thickness of the humerus. However, the principal axis for the comparison between body weight and the average midshaft cortical thickness for the femur is not significantly different from the principal axis for the comparison between body weight and the average midshaft cortical thickness of the humerus, and, therefore, for the subsamples the average midshaft cortical thickness for the femur cannot be strictly interpreted as increasing more rapidly with body weight than does the average midshaft cortical thickness of the humerus. However, in both the comparison between body weight and the average midshaft cortical thickness for the humerus and between body weight and the average midshaft cortical thickness for the femur the Group II sample cannot be distinguished from the Group I sample on the basis of least squares slopes, intercepts or on the basis of the amount of variance left unexplained by the relationship. Therefore, the statistics for the combined Group I and Group II sample for both comparisons are the best characterisations of the trends.

The variance of the average midshaft cortical thickness

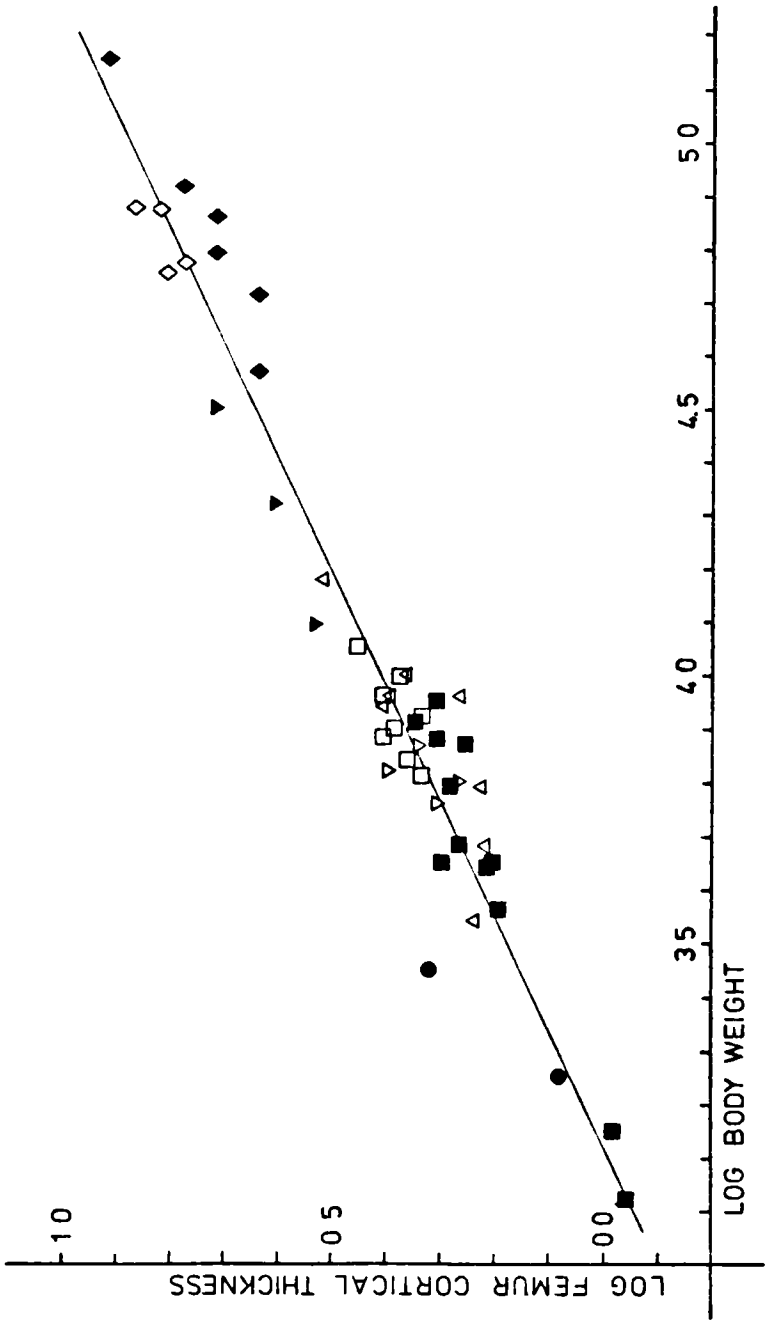

Fig. VI.10. The relationship between body weight and the average cortical thickness of the femur.

Table VI.10.

X = LOG BODY WEIGHT Y = LOG FEMUR CORTICAL THICKNESS

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.47 (.41 - .54)	.38 (.28 - .48)	.46 (.43 - .49)
REDUCED MAJOR AXIS	.49	.40	.47
LEAST SQUARES Y.X	Y = -1.46+.47X	Y = -.99+.37X	Y = -1.44+.46X
SLOPE & 95% C.L.	.47 ± .08	.37 ± .12	.46 ± .03
INTERCEPT & 95% C.L.	-1.46 ± .28	-.99 ± .56	-1.44 ± .13
LEAST SQUARES X.Y	X = 3.18+1.97Y	X = 3.04+2.27Y	X = 3.15+2.10Y
SLOPE & 95% C.L.	1.97 ± .37	2.27 ± .74	2.10 ± .14
INTERCEPT & 95% C.L.	3.18 ± .10	3.04 ± .55	3.15 ± .07
CORRELATION COEFFICIENT	.958	.912	.984
COEF. OF DETERMINATION	.917	.832	.968
UNEXPLAINED VARIANCE Y.X	.0016	.0024	.0021
UNEXPLAINED VARIANCE X.Y	.0069	.0148	.0095
MEAN X	3.74	4.71	4.11
MEAN Y	.29	.74	.46
SAMPLE SIZE	18	12	32

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

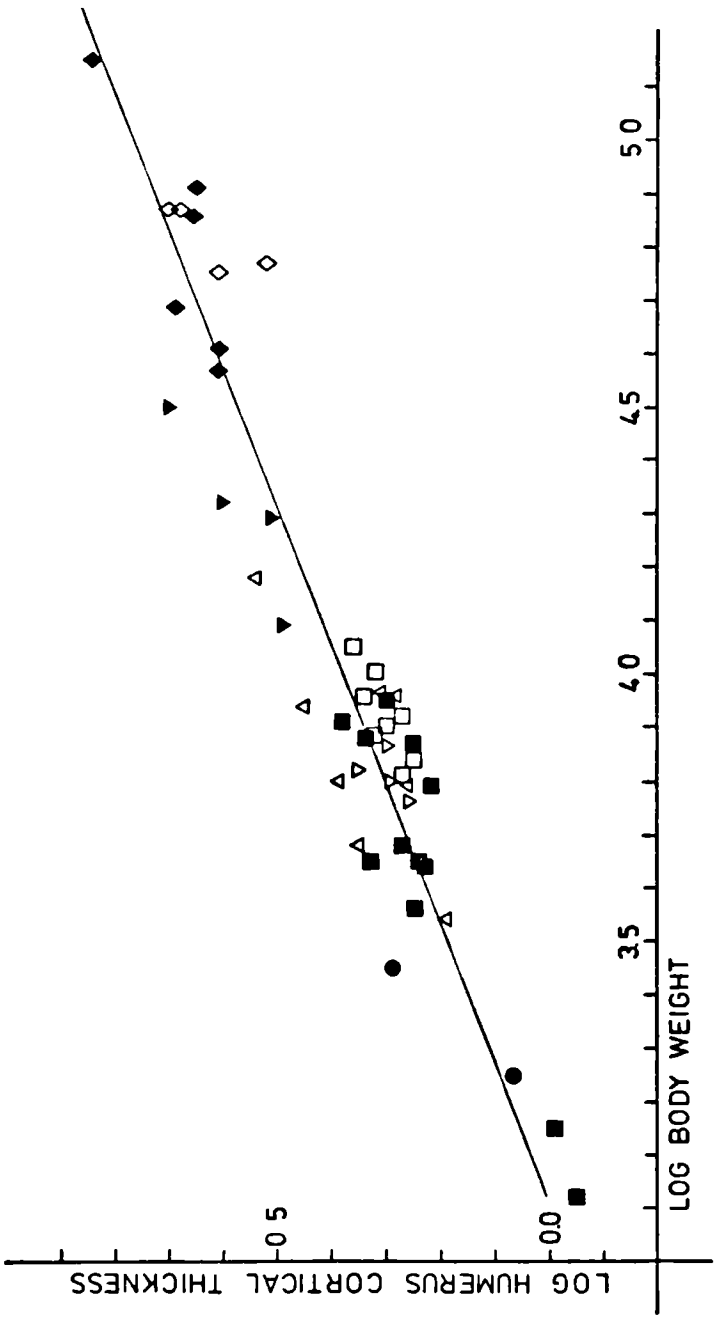

Fig. VI.11. The relationship between body weight and the average cortical thickness of the humerus.

Table VI.11.

X = LOG BODY WEIGHT Y = LOG HUMERUS CORTICAL THICKNESS

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.39 (.31 - .46)	.25 (.14 - .37)	.38 (.35 - .42)
REDUCED MAJOR AXIS	.41	.31	.39
LEAST SQUARES Y.X	Y = -1.15+.38X	Y = -.50+.24X	Y = -1.14+.38X
SLOPE & 95% C.L.	.38 ± .08	.24 ± .14	.38 ± .04
INTERCEPT & 95% C.L.	-1.15 ± .32	-.50 ± .67	-1.14 ± .15
LEAST SQUARES X.Y	X = 3.16+2.25Y	X = 3.13+2.50Y	X = 3.12+2.49Y
SLOPE & 95% C.L.	2.25 ± .51	2.50 ± 1.47	2.49 ± .25
INTERCEPT & 95% C.L.	3.16 ± .14	3.13 ± .94	3.12 ± .11
CORRELATION COEFFICIENT	.921	.775	.967
COEF. OF DETERMINATION	.848	.601	.934
UNEXPLAINED VARIANCE Y.X	.0021	.0034	.0030
UNEXPLAINED VARIANCE X.Y	.0124	.0349	.0197
MEAN X	3.74	4.71	4.11
MEAN Y	.26	.63	.40
SAMPLE SIZE	18	12	32

GROUP 1 — COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 — PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 — GROUP 1 AND GROUP 2

of the femur left unexplained by its relationship to body weight is not significantly different from the variance of the average midshaft cortical thickness of the humerus left unexplained by its relationship to body weight for the combined Group 1 and Group 11 sample. From this, it is possible to conclude that both the average midshaft cortical thickness of the humerus and of the femur were affected to an equal degree by body weight, although due to the locomotor or other differences between the femur and the humerus, there is a more rapid increase in the average midshaft cortical thickness of the femur than there is of the average midshaft cortical thickness of the humerus.

VI. 12. The Relationship Between the Average Midshaft Cortical Thickness of the Femur and the Average Midshaft Cortical Thickness of the Humerus

Fig. VI.12 illustrates the relationship between the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus. The principal axis for the combined sample is positive, indicating that the average midshaft cortcial thickness of the femur is increasing at a significantly more rapid rate than is the average midshaft cortical thickness of the humerus (Table VI.12). The two subsamples when tested independently cannot be distinguished on the bases of least squares slopes, intercepts or the amount of unexplained variance. Therefore, the principal axis for the combined relationship is the best characterisation of the uniform trend across the Group 1 and Group 11 primates.

The comparison between the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus is significantly more variable than the relationship between the circumference of the femur and the circumference of the humerus (Fig. VI. 9). This variability across the sample is due to a highly significant increase in the unexplained variance in the Group 1 sample, indicating that this sample is much more variable in the relationship between the average midshaft cortical thickness of the femur and the average midshaft cortical thickness

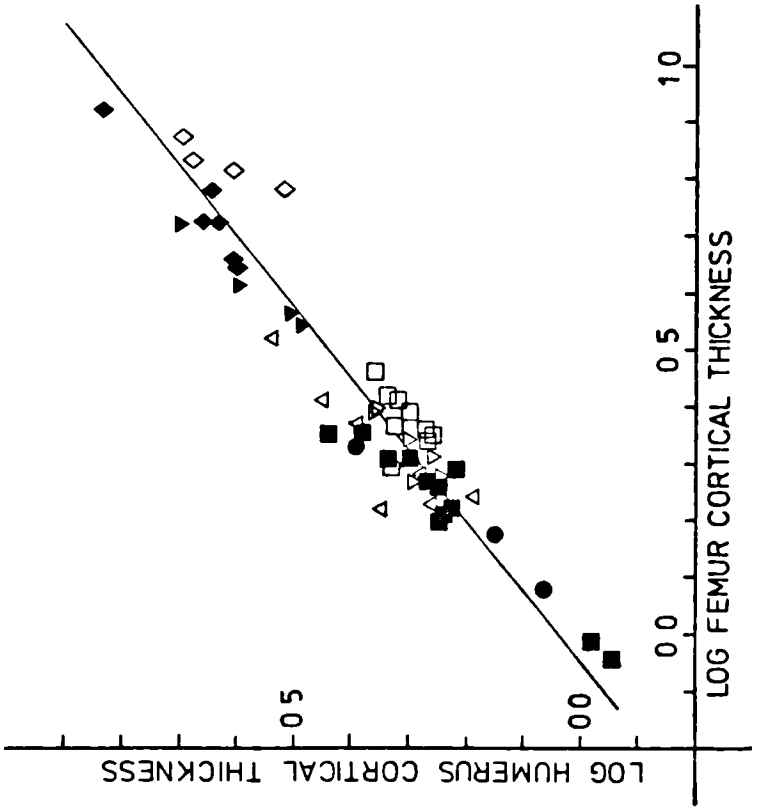

Fig. VI.12. The relationship between the average cortical thickness of the midshaft of the femur and the average cortical thickness of the midshaft of the humerus.

Table VI.12.

X = LOG FEMUR CORTICAL THICKNESS Y = LOG HUMERUS CORTICAL THICKNESS

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.88 (.71 - 1.09)	.70 (.38 - 1.18)	.82 (.75 - .91)
REDUCED MAJOR AXIS	.90	.77	.82
LEAST SQUARES Y.X	Y = .03+.80X	Y = .22+.56X	Y = .04+.80X
SLOPE & 95% C.L.	.80 ± .19	.56 ± .38	.80 ± .09
INTERCEPT & 95% C.L.	.03 ± .06	.22 ± .29	.04 ± .05
LEAST SQUARES X.Y	X = .02+1.00Y	X = .14+.94Y	X = -.01+1.16Y
SLOPE & 95% C.L.	1.00 ± .24	.94 ± .64	1.16 ± .12
INTERCEPT & 95% C.L.	.02 ± .07	.14 ± .41	-.01 ± .06
CORRELATION COEFFICIENT	.895	.727	.963
COEF. OF DETERMINATION	.801	.529	.927
UNEXPLAINED VARIANCE Y.X	.0026	.0040	.0034
UNEXPLAINED VARIANCE X.Y	.0033	.0067	.0050
MEAN X	.29	.74	.45
MEAN Y	.27	.63	.40
SAMPLE SIZE	21	12	31

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

of the humerus than it is in the relationship between the femur circumference and the humerus circumference. In this comparison the Group 1 cercopithecines have a consistently larger average midshaft cortical thickness of the humerus in relation to the average midshaft cortical thickness of the femur than do the colobines and Presbytis. The Group 11 sample is equally variable in the comparison between the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus as it is in the comparison between the femur circumference and the humerus circumference. The same pattern is present in both comparisons. Homo sapiens has both a smaller average midshaft cortical thickness of the humerus and humerus circumference in relation to the remaining Group 11 primates.

VI. 13. The Relationship Between Body Weight and the Idealised Section Modulus of the Femur

Fig. VI.13 illustrates the relationship between body weight and the idealised femur section modulus. The principal axis for the combined sample is significantly positive, indicating that the idealised femur section modulus is increasing more rapidly than is body weight across the sample (Table VI.13). This is also true for the Group 1 primates when tested as an individual sample. The Group 11 sample[15] also characterised by a positive principal axis, however, it does not significantly differ from isometry at the 95% level of significance. The Group 1 sample and the Group 11 sample cannot be distinguished on the basis of their least squares slopes or intercepts, however. Therefore, the positive principal axis of the combined sample can be considered as the best characterisation of a uniform positive increase in the idealised femur section modulus in relation to body weight in the Group 1 and Group 11 primates.

The amount of variance of the idealised femur section modulus explained by its relationship to body weight differs significantly between the Group 1 and Group 11 primates. The Group 11 sample is significantly more variable in relation to

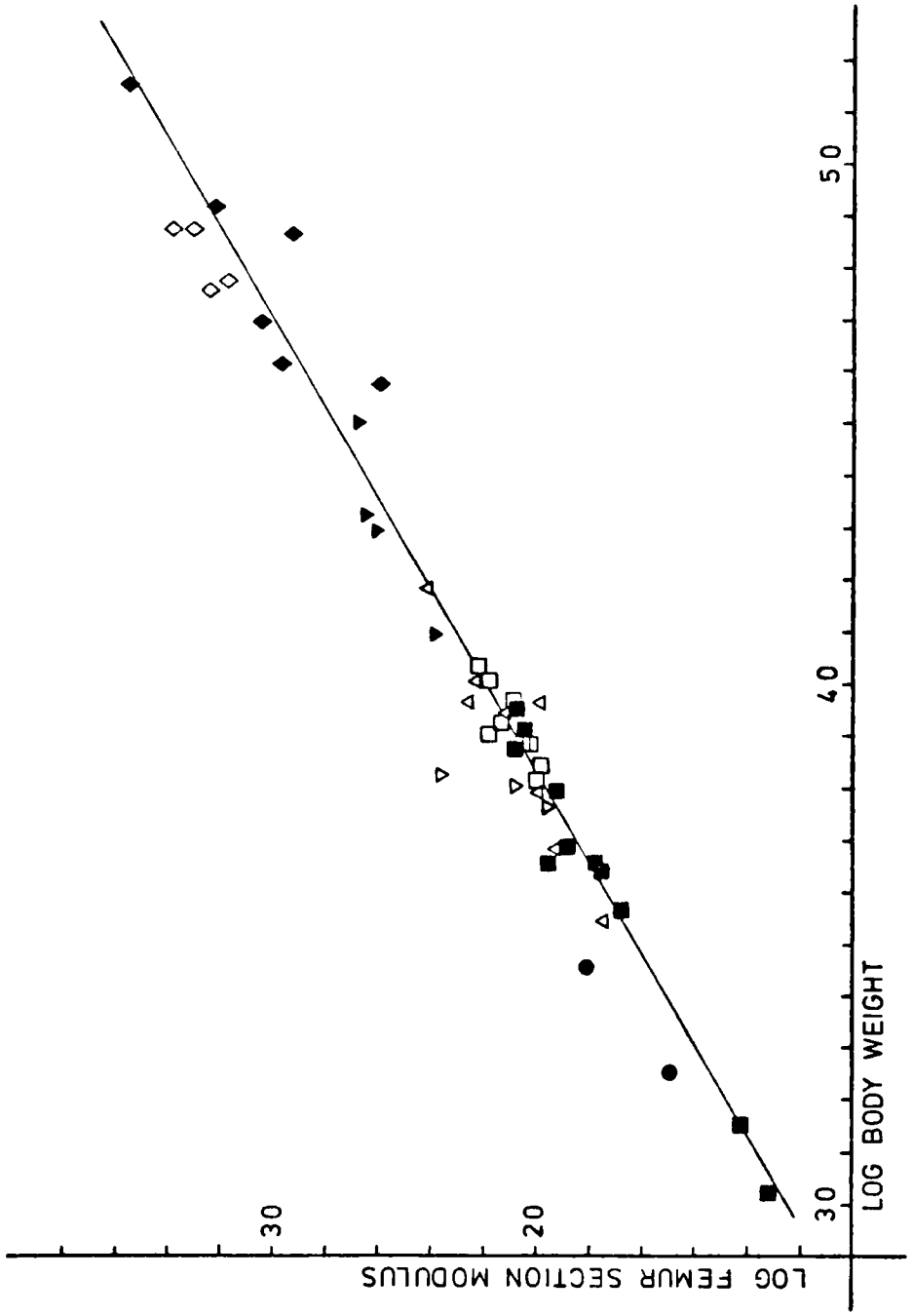

Fig. VI.13. The relationship between body weight and the idealised section modulus of the midshaft of the femur.

Table VI.13.

X = LOG BODY WEIGHT Y = LOG FEMUR SECTION MODULUS

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	1.11 (1.02 - 1.20)	1.27 (.99 - 1.66)	1.17 (1.11 - 1.24)
REDUCED MAJOR AXIS	1.10	1.24	1.17
LEAST SQUARES Y.X	Y = -2.16+1.09X	Y = -2.29+1.13X	Y = -2.41+1.16X
SLOPE & 95% C.L.	1.09 ± .10	1.13 ± .37	1.16 ± .07
INTERCEPT & 95% C.L.	-2.16 ± .38	-2.29 ± 1.74	-2.41 ± .29
LEAST SQUARES X.Y	X = 2.04+.89Y	X = 2.48+.73Y	X = 2.13+.84Y
SLOPE & 95% C.L.	.89 ± .08	.73 ± .24	.84 ± .05
INTERCEPT & 95% C.L.	2.04 ± .16	2.48 ± .73	2.13 ± .13
CORRELATION COEFFICIENT	.985	.911	.988
COEF. OF DETERMINATION	.969	.831	.976
UNEXPLAINED VARIANCE Y.X	.003	.0229	.0103
UNEXPLAINED VARIANCE X.Y	.0025	.0148	.0075
MEAN X	3.74	4.71	4.13
MEAN Y	1.91	3.04	2.36
SAMPLE SIZE	18	12	30

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

body weight than is the Group 1 sample. This suggests that body weight does not relate to the idealised femur section modulus in a constant fashion in both samples. Fig. Vl.13 suggests that the greater unexplained variance in the non-Group ll sample results from the position of Pongo. This primate is characterised by a small idealised femur section modulus in relation to its body weight in comparison to the remainder of the sample. When Pongo is removed from the analysis, the principal axis for the Group ll sample is significantly positive and the two Group 1 and Group ll samples cannot be distinguished on the basis of their least squares slopes, intercepts or on the amount of variance left unexplained by the relationship with body weight.

Vl. 14. The Relationship Between Body Weight and the Idealised Section Modulus of the Humerus

Fig. Vl.14 illustrates the relationship between body weight and the idealised humerus section modulus. The principal axis for the combined Group 1 and Group ll sample is significantly positive (Table Vl.14). This relationship is not significantly different in the least squares slopes, intercepts or the amount of unexplained variance from the relationship between body weight and the idealised femur section modulus (Section Vl.13). Therefore, it can be concluded that across the sample both the idealised femur section modulus and the idealised humerus section modulus increase in an identical fashion with body weight. This is also true when the combined sample is divided into the two subsamples, the Group 1 primates and the Group ll primates. However, in the comparison between body weight and the idealised humerus section modulus, the principal axis for both subsamples are not significantly different from isometry. Taken individually, however, they do not differ in either the least squares slopes or intercepts from the subsample comparisons in the relationship between body weight and the idealised femur section modulus (Table Vl.13). Therefore, it is not possible to reject the hypothesis that both the idealised femur section modulus and the idealised humerus section modulus

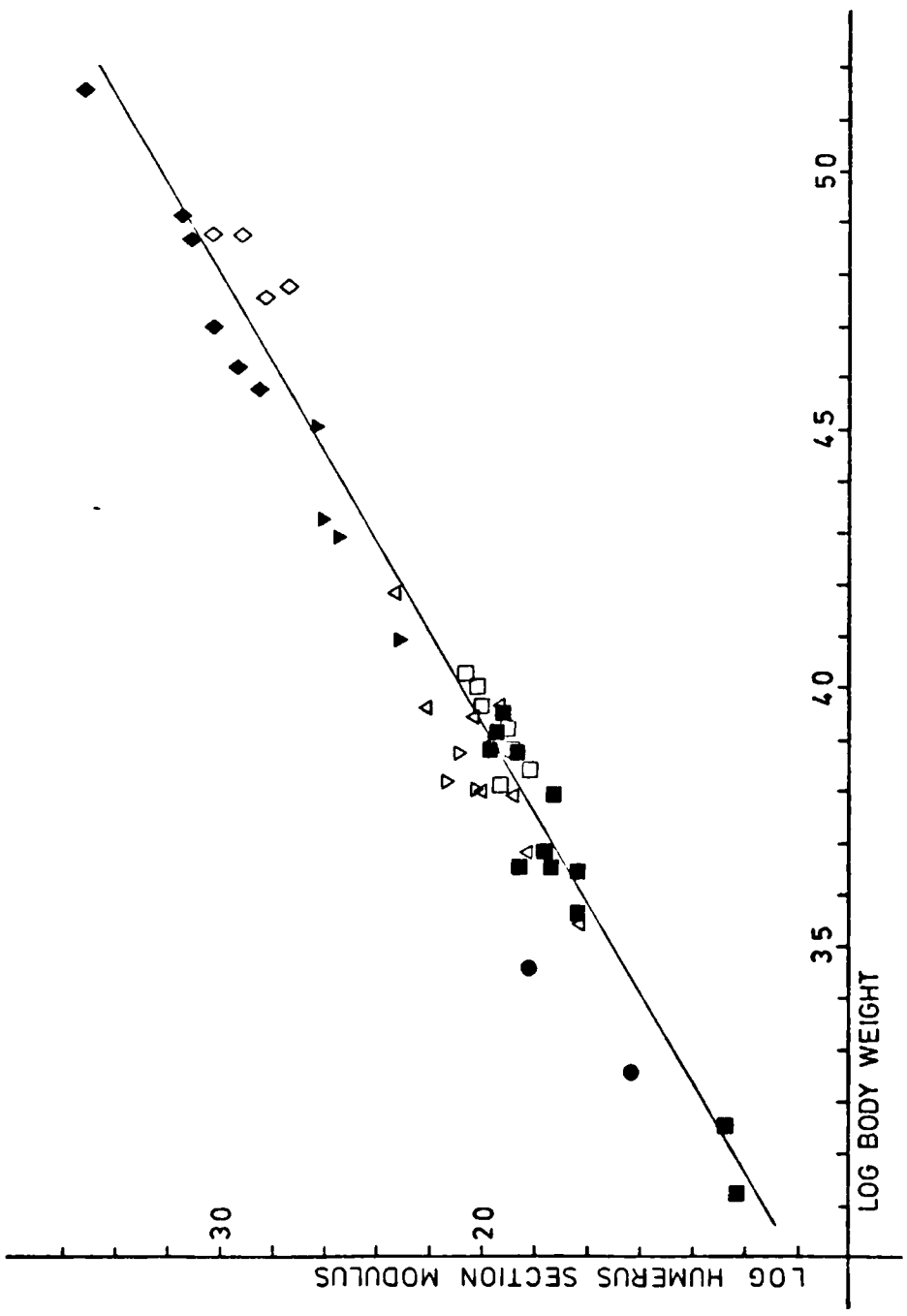

Fig. VI.14. The relationship between body weight and the idealised section modulus of the midshaft of the humerus.

Table VI.14.

X = LOG BODY WEIGHT Y = LOG HUMERUS SECTION MODULUS

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	1.04 (.94 - 1.16)	1.07 (.83 - 1.39)	1.16 (1.10 - 1.23)
REDUCED MAJOR AXIS	1.04	1.07	1.16
LEAST SQUARES Y.X	Y = -2.03+1.02X	Y = -1.65+.97X	Y = -2.49+1.14X
SLOPE & 95% C.L.	1.02 ± .12	.97 ± .31	1.14 ± .07
INTERCEPT & 95% C.L.	-2.03 ± .46	-1.65 ± 1.47	-2.49 ± .30
LEAST SQUARES X.Y	X = 2.09+.94Y	X = 2.21+.86Y	X = 2.23+.85Y
SLOPE & 95% C.L.	.94 ± .11	.86 ± .27	.85 ± .05
INTERCEPT & 95% C.L.	2.09 ± .20	2.21 ± .80	2.23 ± .12
CORRELATION COEFFICIENT	.976	.911	.987
COEF. OF DETERMINATION	.952	.830	.975
UNEXPLAINED VARIANCE Y.X	.0043	.0171	.0107
UNEXPLAINED VARIANCE X.Y	.0039	.0151	.0080
MEAN X	3.74	4.71	4.13
MEAN Y	1.77	2.92	2.23
SAMPLE SIZE	18	12	30

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

increase in the same fashion in relation to body weight in the two subsamples as well as in the combined sample.

This similarity also extends to the amount of variance of the idealised humerus section modulus explained by its relationship to body weight. In this comparison, as with the comparison between body weight and the idealised femur section modulus, the Group II sample is significantly more variable than is the Group I sample. However, inspection of Fig. VI.14 indicates that this is not due to a deviant position for Pongo. All of the pongids, as well as Papio anubis, cluster in a highly correlated trend, which is significantly different from the Group I trend. Homo sapiens deviates from the pongid trend and is consistent with an extension of the Group I trend. Therefore, in this comparison the following conclusions can be drawn

1. The humerii of the pongids have a significantly larger section modulus for their body weights than do the humerii of the Group I primates.
2. Homo is characterised by a smaller idealised humerus section modulus for its body weight than are the remainder of the Group II primates.

VI. 15. The Relationship Between the Idealised Section Modulus of the Femur and the Idealised Section Modulus of the Humerus

The direct comparison of the idealised section modulus of the femur and the idealised section modulus of the humerus (Figs. VI.15 and Table VI.15) illustrates the following points

1. The isometric principal axis characteristic of the Group I primates reflects the identity of the relationship between body weight and the idealised section modulus of the femur and body weight and the idealised section modulus of the humerus in this sample.
2. The position of Papio anubis, Pan and Gorilla indicates a large idealised section modulus of the humerus in relation to the idealised section modulus of the femur.

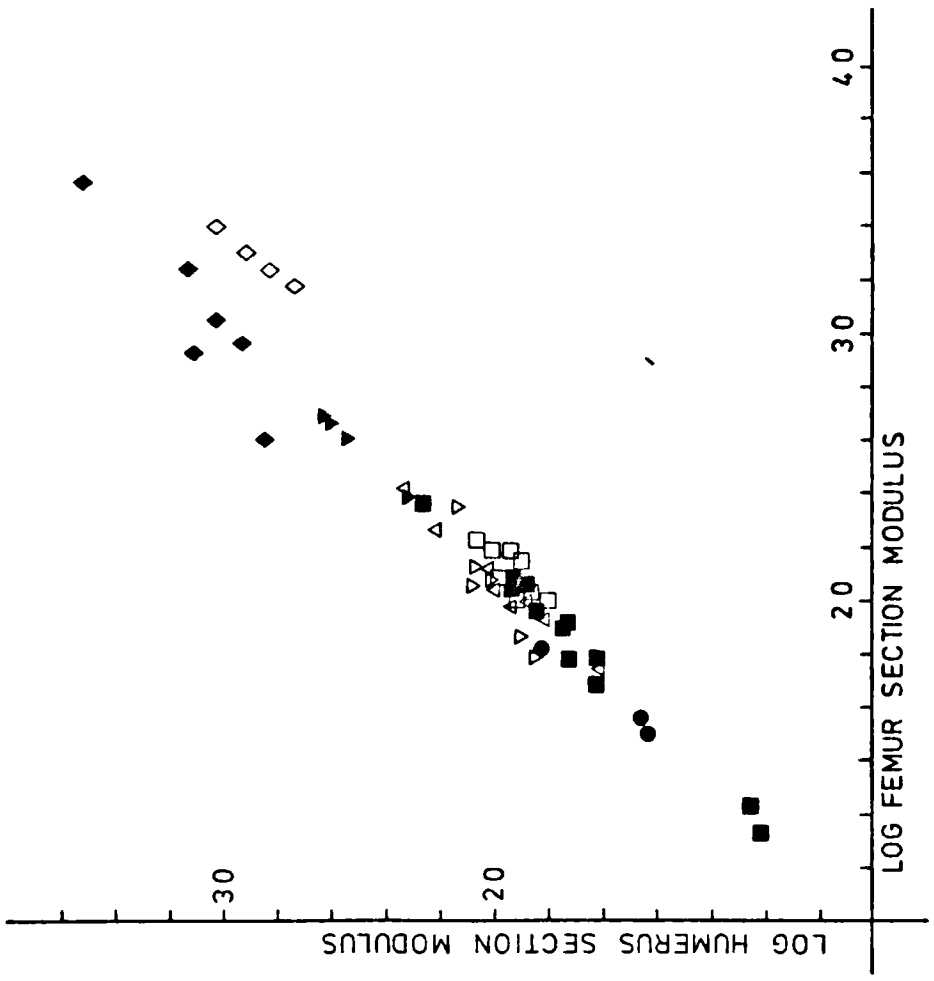

Fig. VI.15. The relationship between the idealised section modulus of the midshaft of the femur and the idealised section modulus of the midshaft of the humerus.

Table VI.15.

X =LOG FE UR SECTION MODULUS Y = L. UMERUS SECTION MODULUS

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.96 (.88 - 1.04)	.32 (.48 - 1.32)	.99 (.92 - 1.0)
REDUCED MAJOR AXIS	.96	.86	.9
LEAST SQUARES Y.X	Y = -.0 + 95X	Y = .93+.65X	Y = -.0 + 97X
SLOPE & 95% C.L.	.95 ± .	.65 ± .39	.97 ± .
INTERCEPT & 95 C.L.	-.04 ± .1	.93 ± 1.19	-. ± .2
LEAST SQUARES X.Y	X = .10+1.02Y	X = .44+.69Y	X = .1 +.9 Y
SLOPE & 95% C.L.	1.02 ± .0	.69 ± .39	± .
INTERCEPT & 9 C.L.	.10 ± .16	.44 ± 1.56	± .19
CORRELATION COEFFICIENT	.984	.764	.9
COEF. OF DETERMINATION	.968	.583	.4
UNEXPLAINED VARIANCE Y.X	.0323	.0414	.0
UNEXPLAINED VARIANCE X.Y	.0331	.0564	.1
MEAN X	1.94	3.04	2.5
MEAN Y	1.80	2.92	2.1
SAMPLE SIZE	21	12	33

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

Their positions are consistent with their positions in the relationship between body weight and the idealised section modulus of the humerus (Fig. VI. 14). These primates have larger than expected humerus section moduli for their body weights based on the Group 1 trend. Their positions in the relationship between the idealised humerus section modulus and the idealised femur section modulus, therefore, result from a relatively large humerus section modulus for their body weights.

3. The positions of Pongo and Homo reflect their positions in the comparisons between body weight and the idealised femur section modulus and the idealised humerus section modulus (Figs. VI. 13 and VI. 14).

Therefore, the identity of the relationships between body weight and the humerus section modulus and body weight and the femur section modulus must be considered to be a statistical illusion. The comparison between the idealised femur section modulus and the idealised humerus section modulus suggests that factors other than, or in addition to, body weight are responsible for the magnitude of both the idealised humerus section modulus and the idealised femur section modulus, at least in the Group II sample.

VI. 16. The Relationship between Body Weight and the Idealised Area of the Cross Section of the Humerus, between Body Weight and the Idealised Area of the Cross Section of the Femur, and between the Idealised Area of the Cross Sect of the Humerus and the Idealised Area of the Cross Section of the Femur

These comparisons show similar relationships as do the corresponding comparisons involving the idealised cross section modulus (Figs. VI. 16, VI. 17, VI. 18, Tables VI. 16, VI. 17, VI. 18). This similarity is to be expected from the high correlation between the idealised section modulus of the femur and the idealised cross section area of the femur and between the idealised section modulus of the humerus and the idealised area of the cross section of the humerus (Sections IV. 4 and IV. 5).

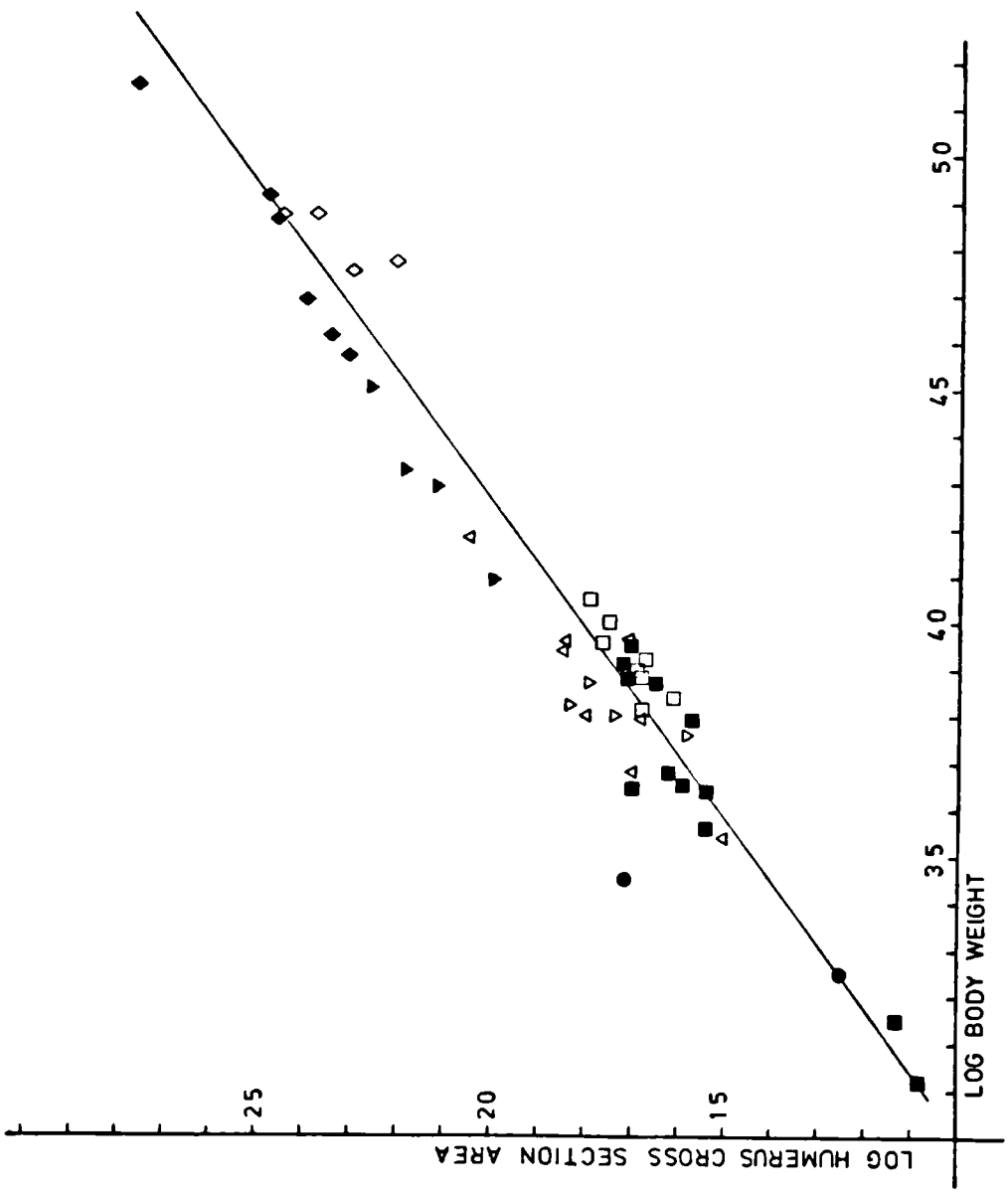

Fig. VI.16. The relationship between body weight and the idealised area of the midshaft of the humerus.

Table VI.16.

X = LOG BODY WEIGHT Y = LOG HUMERUS AREA

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.71 (.61 - .81)	.64 (.47 - .84)	.76 (.71 - .81)
REDUCED MAJOR AXIS	.72	.67	.76
LEAST SQUARES Y.X	Y = -.96+.69X	Y = -.47+.60X	Y = -1.18+.75X
SLOPE & 95% C.L.	.69 ± .11	.60 ± .21	.75 ± .05
INTERCEPT & 95% C.L.	-.96 ± .41	-.47 ± 1.00	-1.18 ± .22
LEAST SQUARES X.Y	X = 1.59+1.34Y	X = 1.57+1.33Y	X = 1.66+1.30Y
SLOPE & 95% C.L.	1.34 ± .21	1.33 ± .47	1.30 ± .09
INTERCEPT & 95% C.L.	1.59 ± .34	1.57 ± 1.11	1.66 ± .18
CORRELATION COEFFICIENT	.958	.894	.984
COEF. OF DETERMINATION	.918	.800	.968
UNEXPLAINED VARIANCE Y.X	.0034	.0079	.0059
UNEXPLAINED VARIANCE X.Y	.0067	.0176	.0102
MEAN X	3.74	4.71	4.13
MEAN Y	1.61	2.36	1.91
SAMPLE SIZE	18	12	30

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

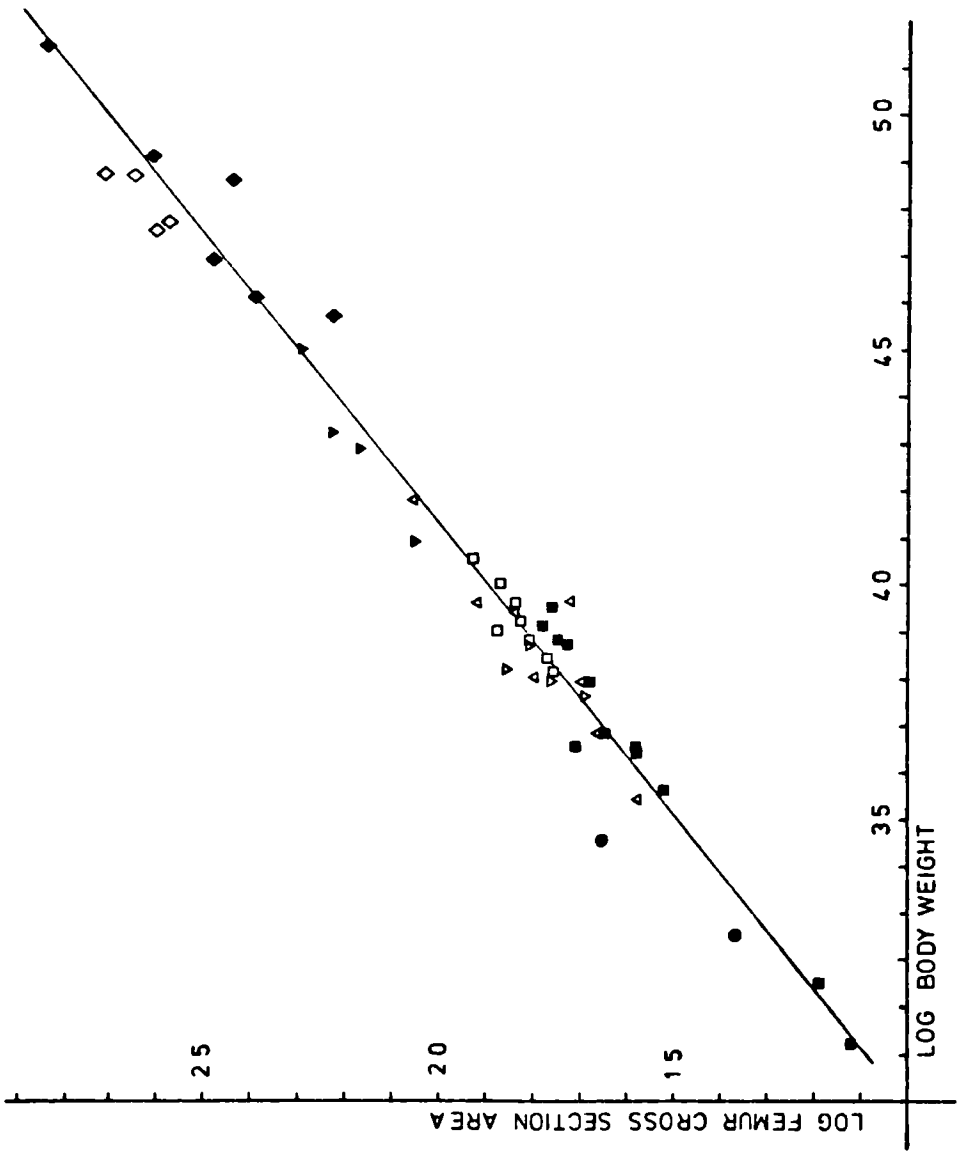

Fig. VI.17. The relationship between body weight and the idealised area of the midshaft of the femur.

Table VI.17.

X = LOG BODY WEIGHT Y = LOG FEMUR AREA

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.80 (.74 - .87)	.80 (.64 - .99)	.82 (.79 - .86)
REDUCED MAJOR AXIS	.80	.81	.83
LEAST SQUARES Y.X	Y = -1.28+.79X	Y = -1.07+.76X	Y = -1.37+.82X
SLOPE & 95% C.L.	.79 ± .08	.76 ± .21	.82 ± .04
INTERCEPT & 95% C.L.	-1.28 ± .28	-1.07 ± .99	-1.37 ± .18
LEAST SQUARES X.Y	X = 1.68+1.23Y	X = 1.84+1.15Y	X = 1.72+1.20Y
SLOPE & 95% C.L.	1.23 ± .12	1.15 ± .32	1.20 ± .06
INTERCEPT & 95% C.L.	1.68 ± .20	1.84 ± .80	1.72 ± .13
CORRELATION COEFFICIENT	.985	.934	.991
COEF. OF DETERMINATION	.969	.871	.983
UNEXPLAINED VARIANCE Y.X	.0016	.0074	.0038
UNEXPLAINED VARIANCE X.Y	.0025	.0113	.0055
MEAN X	3.74	4.71	4.13
MEAN Y	1.68	2.48	2.00
SAMPLE SIZE	18	12	30

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

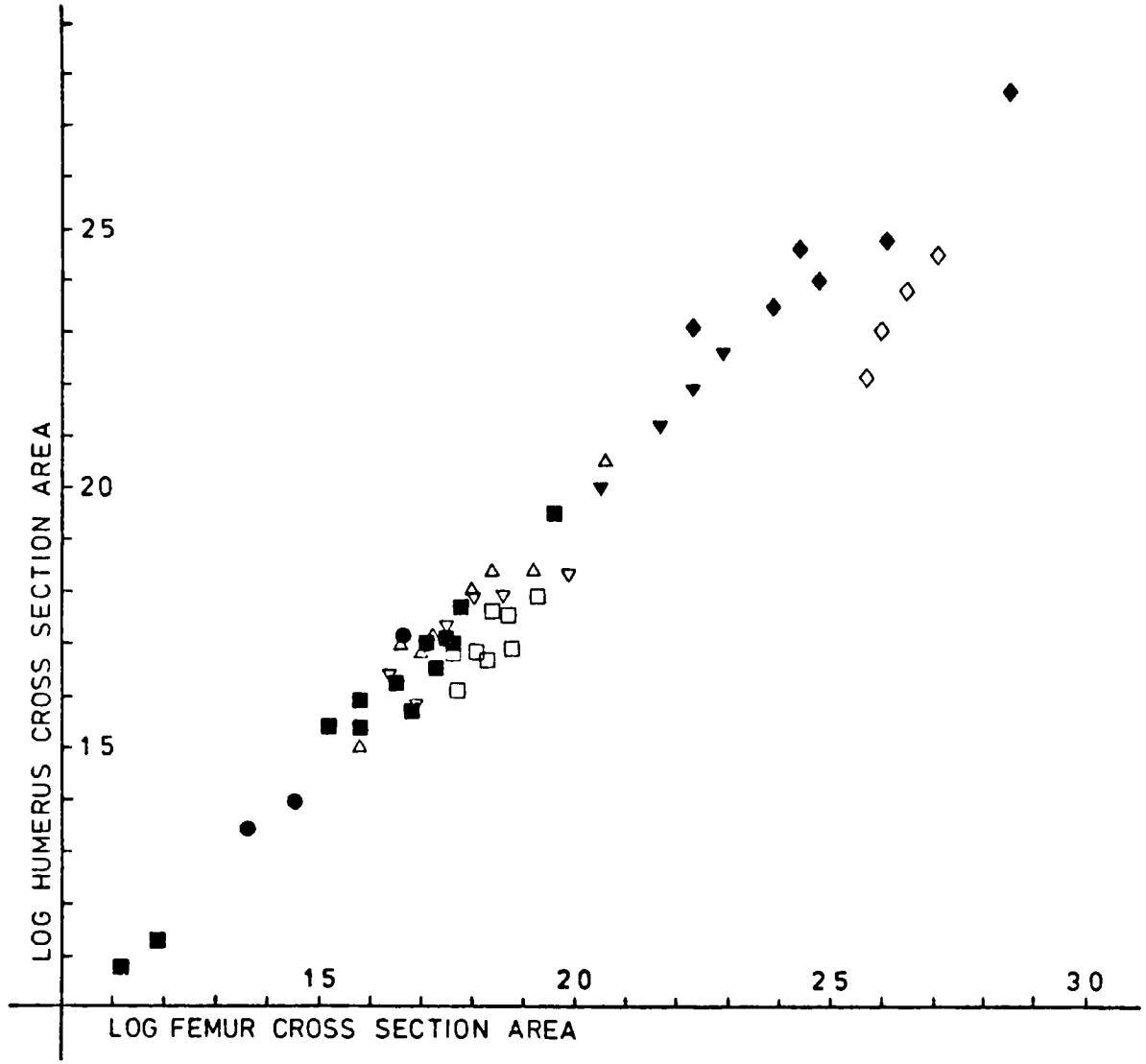

Fig. VI.18. The relationship between the idealised area of the midshaft of the femur and the idealised area of the midshaft of the humerus.

Table VI.18.

X = LOG FEMUR AREA Y = LOG HUMERUS AREA

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	.92 (.82 - 1.04)	.79 (.50 - 1.21)	.91 (.85 - .99)
REDUCED MAJOR AXIS	.93	.83	.71
LEAST SQUARES Y.X	Y = .11+.89X	Y = .71+.66X	Y = .12+.90X
SLOPE & 95% C.L.	.89 ± .12	.66 ± .35	.90 ± .04
INTERCEPT & 95% C.L.	.11 ± .21	.71 ± .88	.12 ± .13
LEAST SQUARES X.Y	X = .01+1.04Y	X = .21+.96Y	X = -.03+1.06Y
SLOPE & 95% C.L.	1.04 ± .14	.96 ± .51	1.06 ± .09
INTERCEPT & 95% C.L.	.01 ± .23	.21 ± 1.21	-.03 ± .17
CORRELATION COEFFICIENT	.962	.799	.977
COEF. OF DETERMINATION	.926	.638	.954
UNEXPLAINED VARIANCE Y.X	.0131	.0143	.0139
UNEXPLAINED VARIANCE X.Y	.0036	.0208	.0090
MEAN X	1.70	2.48	1.79
MEAN Y	1.63	2.36	1.79
SAMPLE SIZE	21	12	53

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

VI. 17. The Robusticity of the Humerus and of the Femur

Section 11.1 describes two separate contexts in which the concept of robusticity has been applied in the interpretation of the size, shape and strength of the long bones in the higher primates. The first context refers to the relationship between body size and the diameter or circumference of the cross section of a long bone. The second context refers to the relationship between the length of the bone and the diameter or circumference of its cross section. Table VI.19 summarises the statistics for humerus robusticity, and Table VI.20 summarises the statistics for femur robusticity in both of these contexts.

All of the measurements of the size of the cross section of the humerus relate to body weight in a similar fashion. In the Group 1 primates all of the measurements are isometric with body weight. This is also true for the Group 11 primates when they are taken as an independent sample. However, when the Group 1 and the Group 11 primates are taken as a combined sample, all of the comparisons except that between body weight and the transverse diameter of the humerus are positively allometric The principal axis for this comparison is just not significantly different from isometry at the 95% level of significance. This suggests a similar pattern to that observed in the other cross section measurements. Therefore, no matter whether the size of the cross section of the humerus is measured by the external measurements or by measurements which incorporate the cortical thickness and are meant to represent the strength of the cross section, the general allometric patterns are similar within the particular samples tested.

When humerus robusticity is taken in the context of the relationship between body weight and the size of the cross section (the transverse diameter of the cross section, the sagittal diameter of the cross section or the circumference of the cross section) or between body weight and the strength of the cross section (the section modulus or the area) the allometric relationship is, therefore, isometric within the Group 1 and Group 11

HUMERUS									
	Group I			Group 2			Group 1 & 2		
Comparison	N	P.a. & 95% C.L.	r	N	P.a. & 95% C.L.	r	N	P.a. & 95% C.L.	r
x = body weight y = transverse diameter	20	.29(.23-.35)	.907	12	.35(.26-.44)	.909	32	.35(.33-.38)	.977
x = body weight y = sagittal diameter	20	.35(.31-.39)	.972	12	.34(.26-.43)	.916	32	.41(.38-.43)	.987
x = body weight y = circumference	20	.32(.29-.36)	.969	12	.33(.24-.42)	.901	33	.37(.34-.39)	.986
x = body weight y = cortical thickness	18	.39(.31-.46)	.921	12	.25(.14-.37)	.775	32	.38(.35-.42)	.967
x = body weight y = cross section area	18	.71(.61-.81)	.958	12	.64(.47-.84)	.894	30	.76(.71-.81)	.984
x = body weight y = section modulus	18	1.04(.94-1.16)	.976	12	1.07(.83-1.39)	.911	30	1.16(1.10-1.23)	.987
x = body weight y = length	20	.33(.30-.37)	.973	12	.33(.30-.37)	.982	33	.37(.36-.39)	.993
x = circumference y = length	20	1.02(.94-1.11)	.982	12	.95(.77-1.16)	.940	32	1.01(.97-1.06)	.993

Table VI.19. Statistics for the robusticity of the humerus. N = sample size. P.a. = principal axis. 95% C.L. = 95% confidence limits for the principal axis. r = correlation coefficient. Group 1 = Colobus, Presbytis, Cercopithecus and Cercocebus. Group 2 = Papio, Pan, Pongo, Gorilla and Homo.

FEMUR									
	Group 1			Group 2			Group 1 & 2		
Comparison	N	P.a. & 95% C.L.	r	N	P.a. & 95% C.L.	r	N	P.a. & 95% C.L.	r
x = body weight[1] y = transverse diameter	20	.35(.32-.39)	.972	12	.40(.34-.47)	. 63	32	.39(.38-.41)	.992
x = body weight y = sagittal diameter	20	.35(.31-.38)	.974	12	.39(.26-.53)	.859	32	.37(.35-.40)	.978
x = body weight y = circumference	20	.34(.31-.37)	.984	12	.37(.29-.46)	.924	33	.37(.35-.39)	.989
x = body weight y = cortical thickness	18	.47(.41-.54)	.958	12	.38(.28-.48)	.912	30	.46(.43-.49)	.984
x = body weight y = cross section area	18	.80(.74-.87)	.985	12	.80(.64-.99)	.934	30	.82(.79-.86)	.991
x = body weight y = section modulus	18	1.11(1.02-1.20)	.985	12	1.27(.99-1.66)	.911	30	1.17(1.11-1.24)	.988
x = body weight y = length	20	.37(.33-.41)	.968						
x = circumference y = length	20	1.11(1.03-1.20)	.986						

Table VI.20. Statistics for the robusticity of the femur. N = sample size. P.a. = principal axis. 95% C.L. = 95% confidence limits for the principal axis. r = correlation coefficient. Group 1 = Colobus, Presbytis, Cercopithecus and Cercocebus. Group 2 = Papio, Pan, Pongo, Gorilla and Homo.

primates and is positively allometric when these samples are taken together.

In order to interpret the robusticity of the humerus in the second context, the relationship between the cross section of the humerus and the length of the humerus, it is necessary to take into consideration the relationship between body weight and the length of the humerus. Table IV.19 also provides the statistics for this comparison in the Group I and Group II primates and in the combined Group I and Group II sample. The pattern in this comparison is identical to that observed in the comparisons between body weight and the size and strength of the cross section of the humerus. The length of the humerus is isometric with body weight when the Group I and Group II primates are taken as independent samples and is positively allometric with body weight when the samples are combined. The comparison between the circumference of the humerus (the most frequently used measurement of the cross section of the humerus in robusticity comparisons) and humerus length (Fig. VI.19) reflects the similar allometric relationship of both of these variables with body size across the sample. The comparison between the circumference of the humerus and the length of the humerus is isometric not only within the Group I and Group II primates when they are tested separately, but is also isometric when the samples are combined. This isometric relationship in the combined sample results from the similar positive allometric relationship of both of these variables with body weight.

The robusticity relationships of the femur are fundamentally different from those of the humerus in the Group I primates. Table VI.20 shows that although external measurements of the size of the cross section (the transverse diameter, the sagittal diameter and the circumference) are isometric with body weight in the Group I primates, the strength measurements of the cross section are positively allometric with body weight. Therefore, in the Group I primates the strength of the cross section increases more rapidly in relation to body weight than do the external measurements of the cross section.

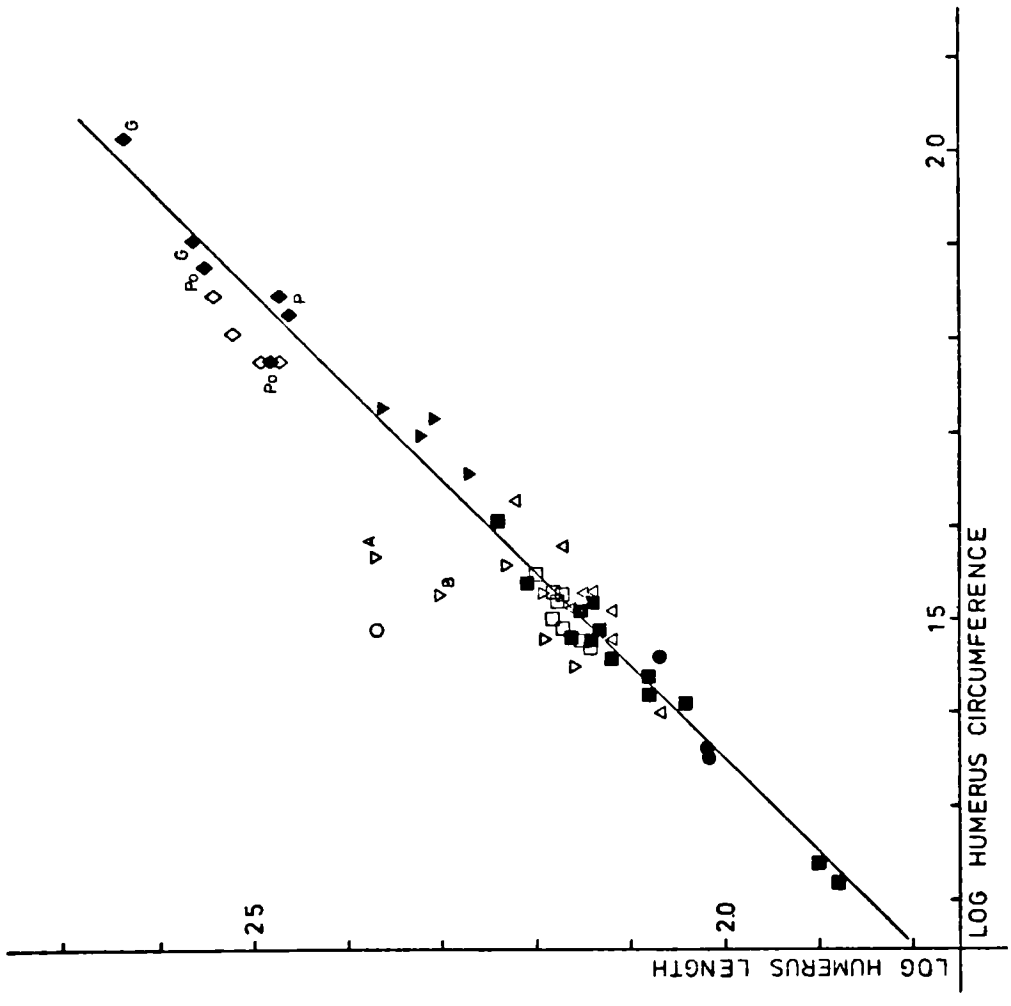

Fig. VI.19. The relationship between the length of the humerus and the circumference of the humerus.

Table VI.21.

X = LOG HUMERUS CIRCUMFERENCE Y = LOG HUMERUS LENGTH

	GROUP 1	GROUP 2	GROUP 3
PRINCIPAL AXIS	1.02 (.94 - 1.11)	.95 (.77 - 1.16)	1.01 (.97 - 1.06)
REDUCED MAJOR AXIS	1.02	.94	1.01
LEAST SQUARES Y.X	Y = .66+1.00X	Y = .87+.89X	Y = .65+1.01X
SLOPE & 95% C.L.	1.00 ± .10	.89 ± .23	1.01 ± .05
INTERCEPT & 95% C.L.	.66 ± .14	.87 ± .41	.65 ± .07
LEAST SQUARES X.Y	X = -.58+.97Y	X = -.66+1.00Y	X = -.62+.98Y
SLOPE & 95% C.L.	.97 ± .09	1.00 ± .25	.98 ± .05
INTERCEPT & 95% C.L.	-.58 ± .20	-.66 ± .63	-.62 ± .10
CORRELATION COEFFICIENT	.982	.940	.993
COEF. OF DETERMINATION	.964	.884	.985
UNEXPLAINED VARIANCE Y.X	.00031	.0012	.00063
UNEXPLAINED VARIANCE X.Y	.00030	.0013	.00061
MEAN X	1.46	1.82	1.60
MEAN Y	2.12	2.49	2.26
SAMPLE SIZE	20	12	32

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOCEBUS

GROUP 2 PAPIO, PAN, PONGO, GORILLA, HOMO

GROUP 3 GROUP 1 AND GROUP 2

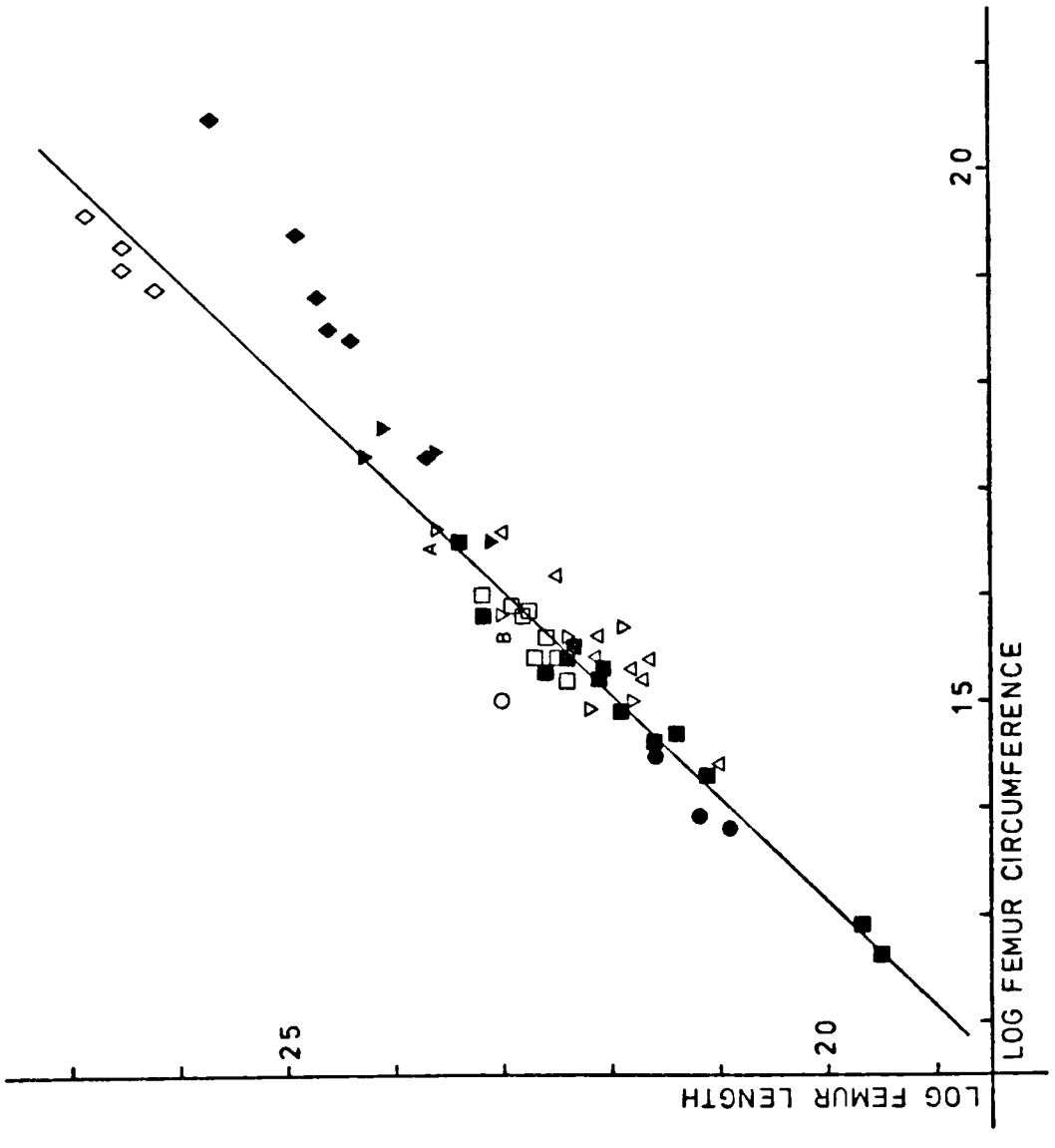

Fig. VI.20. The relationship between the length of the femur and the circumference of the femur.

Table VI.22.

X = LOG FEMUR CIRCUMFERENCE Y = LOG FEMUR LENGTH

	GROUP 1
PRINCIPAL AXIS	1.11 (1.03 - 1.20)
REDUCED MAJOR AXIS	1.11
LEAST SQUARES Y.X	Y = .56+1.09X
SLOPE & 95% C.L.	1.09 ± .09
INTERCEPT & 95% C.L.	.56 ± .14
LEAST SQUARES X.Y	X = -.46+.89Y
SLOPE & 95% C.L.	.89 ± .08
INTERCEPT & 95% C.L.	-.46 ± .17
CORRELATION COEFFICIENT	.986
COEF. OF DETERMINATION	.972
UNEXPLAINED VARIANCE Y.X	.0003
UNEXPLAINED VARIANCE X.Y	.00025
MEAN X	1.51
MEAN Y	2.21
SAMPLE SIZE	20

GROUP 1 COLOBUS, PRESBYTIS, CERCOPITHECUS, CERCOLEBUS

Although the pattern observed in the Group I primates is discernable in the Group II primates, the relationship between body weight and both the external measurements of the cross section of the femur and the strength measurements of the cross section of the femur are ambiguous. All of the external measurements of the cross section of the femur are isometric with body weight except for the transverse diameter. The measurement is just significantly different from isometry. Both of the strength measurements of the cross section have a positive principal axis, however, both of these principal axes are just not significantly different from isometry at the 95% level of significance.

In the combined Group I and Group II sample all of the comparisons between body weight and the external measurements of the cross section of the femur are significantly positive.

Therefore, the major difference in the comparisons between body weight and the size and the strength of the cross section of the femur and between body weight and the size and the strength of the cross section of the humerus is found among the Group I primates. In these primates, the strength measurements of the cross section of the femur are positively allometric in relation to body weight while the strength measurements of the cross section of the humerus are isometric with body weight as are the external measurements of both the cross section of the femur and the cross section of the humerus.

Sections IV.3 and IV.4 have argued that this would be the expected tendency across the combined Group I and Group II sample. Femur cortical thickness is strongly positively allometric with body weight across the combined sample, as it is with all of the external measurements of the size of the cross section of the femur. Therefore, the strength measurement which incorporates cortical thickness would be expected to increase at a faster rate in relation to body size than would the external measurements of the cross section of the femur.

Although all of the comparisons between body weight and the size or strength of the cross section are positively allometric

in the combined Group 1 and Group 11 sample, the strength measurements have a higher principal axis with body weight than do the external measurements of the cross section. It, therefore, can be concluded that the external measurements of the cross section of the femur do not reflect the magnitude of the strength of the cross section of the femur in either compression or bending. When these external measurements are used in robusticity analyses for the specific purpose of supporting or refuting theoretically based mechanical models of bone allometry, they would be expected to produce inaccurate conclusions.

However, if the purpose of the robusticity analyses is to recognise general patterns of allometric relationship across the higher primates rather than to support or refute theoretically based mechanical models of bone allometry, they can be a valuable interpretive tool. The previous sections have presented results relevant to robusticity in the context of the relationship between the size of the cross section and body weight. Among the significant results of these analyses is the general consistency in the size of the cross section of both the humerus and the femur with body weight in the Group 1 or smaller bodied primates. This consistency is even true for primates such as Hylobates, which have elongated limbs in relation to their body weight. There is also the remarkable consistency in the shape of the cross section of the femora of these primates in spite of quite different locomotor patterns found among them. Although there is a marked difference in the shape of the humerus among these primates, the amount of bone material present in the cross section of this bone, as measured by the circumference of the cross section or by the average area of the cross section, is surprisingly consistent across the sample. These results as well as those in reference to the Group 11 primates will be fully discussed in Chapter IX.

Robusticity comparisons in the context of the relationship between the length of a long bone and the size of its cross section

can also produce useful results. Fig. VI.20 illustrates the relationship between the circumference of the midshaft of the femur (the most frequently used measurement in such robusticity comparisons) and the length of the femur. The Group 1 primates are characterised by a significantly positive principal axis (Table VI.22) which indicates that the length of the femur is increasing at a faster rate than is the circumference of the femur. The low unexplained variance for this comparison emphasises the consistency of this pattern among these primates. The significant deviation of Hylobates from the Group 1 trend is consistent with the position of this primate in the comparisons between body weight and the length of the femur and between body weight and the circumference of the midshaft of the femur. These results indicate that the position of Hylobates in the comparison between the circumference of the femur and the length of the femur results from a longer than expected femur for body weight based on the Group 1 trend.

The positions of the great apes in this comparison also reflect their positions in the comparisons between body weight and femur length and between body weight and femur circumference. Their significantly robust femora in comparison with the Group 1 primates result from shorter than expected femora for their body weights. Fig. VI.20 also illustrates the similarity in the femur proportions of Homo sapiens and the Group 1 primates.

Fig. VI.19 illustrates the relationship between the circumference of the midshaft of the humerus and the length of the humerus. There is a highly correlated isometric principal axis which characterises not only the Group 1 primates but also the combined Group 1 and Group II sample (Table VI.21). This indicates a remarkable consistency in humerus proportions across the sample in spite of marked locomotor differences which characterise these primates. Of particular interest in this context is the similarity in humerus proportions characterising Homo sapiens and Pongo.

The only outlying primate in this comparison is Hylobates.

This primate is characterised by an extremely gracile humerus. This results from the greatly elongated humerus for body weight. Currey (1967) has suggested that the gracile humerus of the gibbons is a function of its arm swinging, or brachiating form of locomotion, a locomotor pattern which would avoid the combination of compressive and bending stresses to which the humerus of quadrupedal primates would be subjected. This point will be discussed in greater detail in Chapter IX.

VII. The Allometry of Limb Bones in Fossil Primates

VII. 1. Introduction

In this chapter, the limb proportions of fossil primates are analysed in relation to the proportional relationships of the extant primates determined in Chapters V and VI. Table III.3 gives both the fossils as well as the measurements which are used in the analysis. With the exception of the Maboko humerus and femur, which were measured by the author, measurements are gathered from the literature and, where possible, checked on casts.

There are eight comparisons from the preceding chapters against which the limb proportions of fossil primates can be compared without recourse to body weight. Because body weight for the fossils is predicted from the transverse diameter of the femur, the length of the humerus and the circumference of the humerus (Chapter VIII), use of comparisons involving body weight would be redundant to comparisons involving the measurements themselves. There are eight relevant comparisons

1. The relationship between the circumference of the humerus and the circumference of the femur.
2. The relationship between the length of the femur and the circumference of the femur.
3. The relationship between the length of the humerus and the circumference of the humerus.
4. The relationship between the length of the femur and the length of the tibia.
5. The relationship between the length of the femur and the length of the humerus.
6. The relationship between the length of the humerus and the length of the radius
7. The relationship between the length of the tibia and the length of the radius.
8. The relationship between the length of the hindlimb and the length of the forelimb.

VII. 2. The Relationship Between the Circumference of the Femur and the Circumference of the Humerus

Fig. VII.1 illustrates the relationship between femur circumference and humerus circumference and includes not only the extant Group I and Group II primates but also the available New World primates (Appendix I) and the four fossil specimens with both humerus circumference and femur circumference (Table III. 3).The maprity of the New World primates fall within the expected trend. The exception is Alouatta senicules (male). This specimen has a femur circumference just below the 95% confidence limits for the expected femur circumference predicted from the humerus circumference with reference to this trend. However, because Alouatta senicules (female) falls comfortably within the expected confidence limits and because the male is a single specimen, little importance is given to this deviation. Among the fossils both Pliopithecus vindobonensis and Dendropithecus macinnesi fall comfortably within the confidence limits for the Old World primates. However, they both have humerus circumferences slightly larger than the predictions based on this trend, a characteristic shared with Hylobates, the majority of the New World primates, Papio anubis, Pan and Gorilla. Mesopithecus pentelici is significantly different from this trend and has a femur circumference significantly larger than the expected circumference for its body weight. A large femur circumference in relation to humerus circumference is also found in Homo.

VII. 3. The Relationship Between the Length of the Femur and the Circumference of the Femur

Fig. VII. 2 illustrates the relationship between femur length and femur circumference including the Group I and Group II primates as well as the New World primates and the available fossil specimens. With the exception of Lagothrix all of the New World primates are not significantly different from the combined Group I and Group II trend. Lagothrix has an extremely short femur for its femur circumference.

Among the fossil primates, Dendropithecus, Australopithecus Proconsul sp. (Maboko), KNM-ER-1481 and KNM-ER-1472 are not

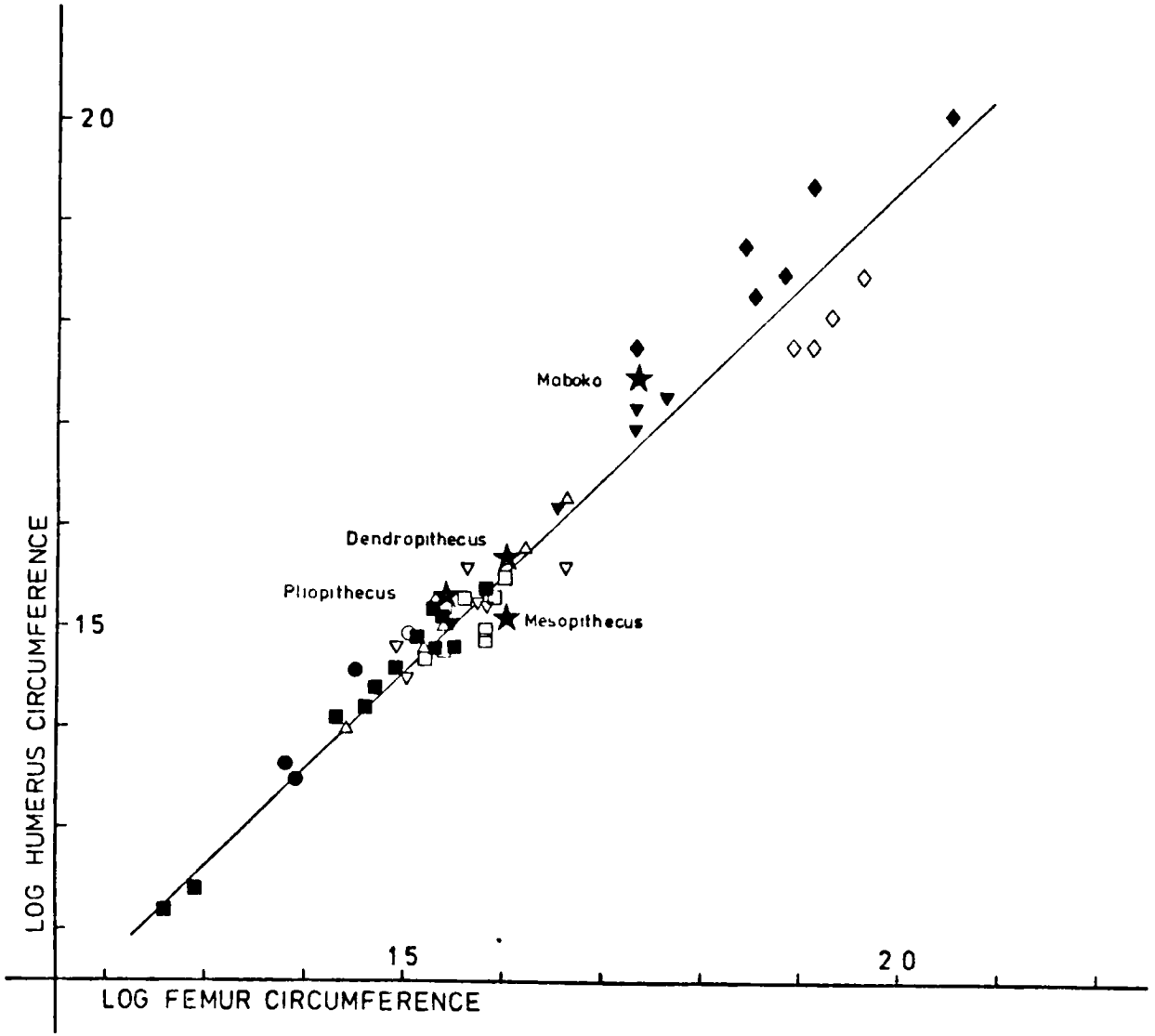

Fig. VII. 1. The relationship between the circumference of the femur and the circumference of the humerus including selected fossil higher

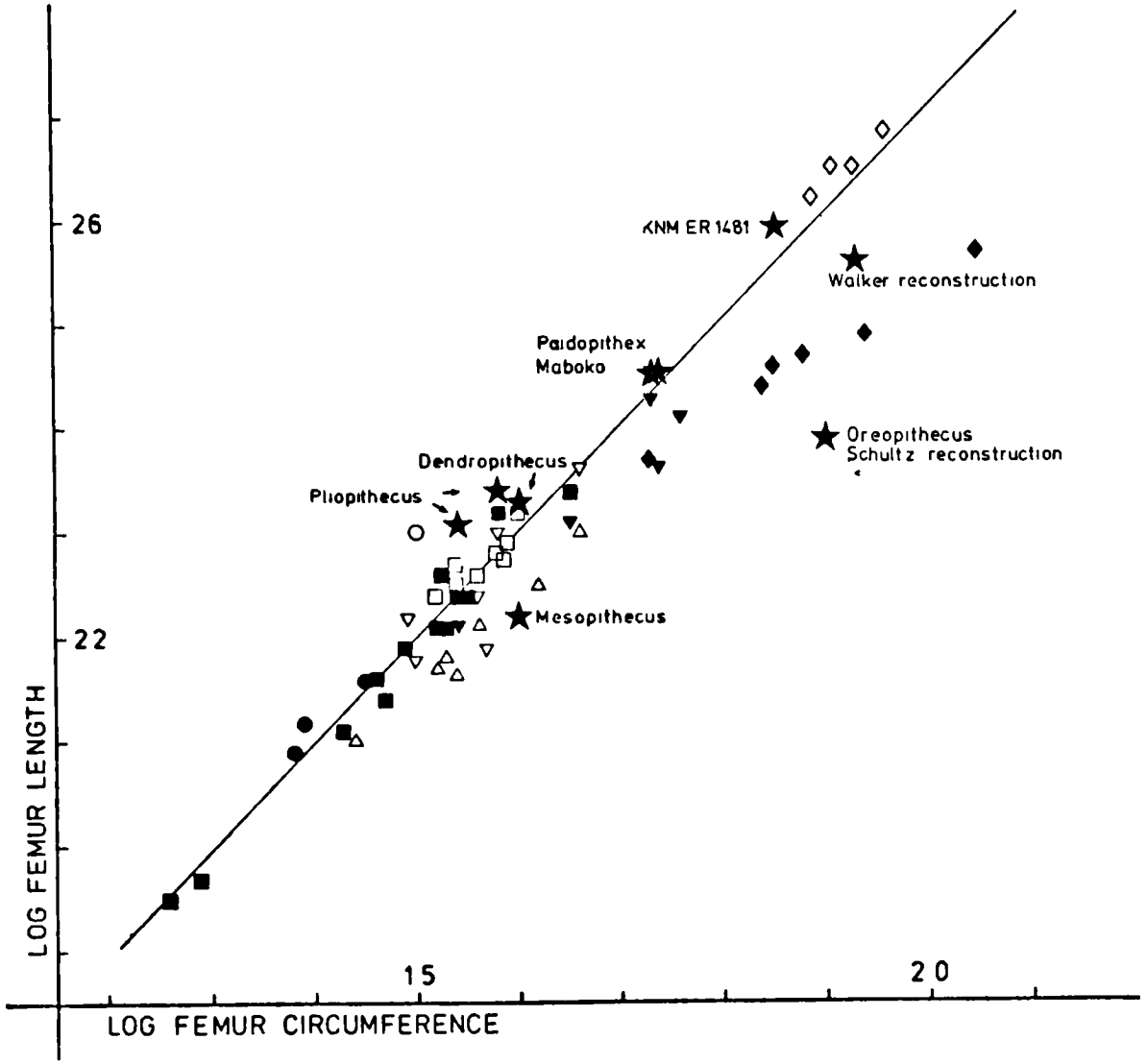

Fig. VII.2.

The relationship between the circumference of the femur and the length of the femur including selected fossil higher primates.

significantly different from the Group 1 and Group 11 trend. The significantly deviant fossils are Pliopithecus, Mesopithecus, and Oreopithecus.

1. Pliopithecus - the position of Pliopithecus is ambiguous. Section V11.1 has shown that although the relationship between humerus circumference and femur circumference for Pliopithecus (Ind. 11) is not significantly different from the expected Group 1 trend, it lies on the limits of that trend and has a femur circumference which is small for its expected humerus circumference, or conversely a humerus circumference which is large for its expected femur circumference. Without an independent measure of body size it is difficult to determine which of the choices is accurate. However, based on the significantly higher correlation between femur circumference and body weight than between humerus circumference and body weight in the Group 1 primates (Section V1. 9) it would be reasonable to postulate that the femur circumference was an accurate reflection of body weight in Pliopithecus and that the deviation in the relationship between humerus circumference and femur circumference resulted primarily from a larger than expected humerus circumference for the femur circumference. A second line of evidence supporting this argument is the high correlation between humerus length and humerus circumference (Section V1.18) indicating that the longer the humerus in a primate the relatively larger will be its humerus circumference. Section V11. 6 shows that Pliopithecus has a humerus which is elongated in relation to its femur length, and, therefore by inference, in relation to its body weight. These two lines of argument are true for Hylobates, as well as the majority of the New World primates. If this line of reasoning is correct, the deviation in the position of Pliopithecus in the

relationship between femur length and femur circumference is the result of the lengthening of the femur and not a reduction in the size of the femur circumference.

2. Mesopithecus - Mesopithecus has a significantly larger femur circumference for its femur length, or conversely, a significantly short femur length for its femur circumference. It is difficult to decide between these alternatives for Mesopithecus. It is identical to the Group 1 primates in the proportional relationships of the lengths of its long bones(Figs. VII. 6 and VII. 7). However, these primates are also consistent in having a smaller femur circumference for their body weights than does Mesopithecus, and they are also primarily arboreal in their locomotor behaviour. In the relationship between femur circumference and femur length, Mesopithecus is most similar to the individuals available for analysis from the genus Macaca. Data are not sufficient at present to argue whether or not the femur robusticity in Macaca results from a short hindlimb for body weight or from a larger femur circumference for body weight. Delson (1975) argues that Mesopithecus was a ground dwelling primate occupying a similar habitat to the modern Macaca. On present evidence, it can only be suggested that the robust femur that is characteristic of both Mesopithecus and Macaca is a feature found in terrestrial or semi-terrestrial primates of their general body weights. However, the significance of the feature is not clear.

3. Oreopithecus - the extremely deviant position of Oreopithecus in the relationship between femur length and femur circumference can best be interpreted as the function of an improperly reconstructed femur circumference. In arriving at the figure of

79 mm for the circumference, Schultz (1960) took the transverse diameter of the shaft at the midpoint (transverse diameter = 25 mm) and applied the formula for the circumference of a circle ($C = \pi d$). The major difficulty lies with the deformed condition of the cross section of the shaft. There is considerable anterior-posterior compression, which can be assumed to have exaggerated the magnitude of the transverse diameter. In addition, it cannot be assumed that the shaft was round. On the basis of the consistency between shaft circumference and femur length in the Pongidea and on the specific proportional relationship between Oreopithecus and Pongo, a shaft circumference of approximately 57 mm would be a reasonable estimate.

VII. 4. The Relationship Between the Length of the Humerus and the Circumference of the Humerus

Fig. VII.3 illustrates the relationship between humerus length and humerus circumference in the Group I and Group II primates, the New World primates and the fossil primates. Of the fossils only Mesopithecus, Proconsul sp. (Maboko), Dryopithecus fontani and interpretation 1 for Austriacopithecus (Chapter III) are not significantly different from the Group I and Group II trends. Dendropithecus, Pliopithecus and Proconsul africanus are significantly different from this trend. They all deviate in the direction of an elongated humerus in relation to their humerus circumferences. This is a pattern similar to that characteristic of the New World primates, Alouatta and Lagothrix, that engage in below branch feeding behaviour.

Pliopithecus and Dendropithecus for which there are femora and humerii from the same individual, are also similar to Alouatta and Lagothrix in the comparison between the lengths of these bones (Fig. VII.5). Proconsul africanus lacks a femur and, therefore, it is impossible to include it in the comparison between humerus length and femur length. However, the similarity between Proconsul africanus and both Pliopithecus and

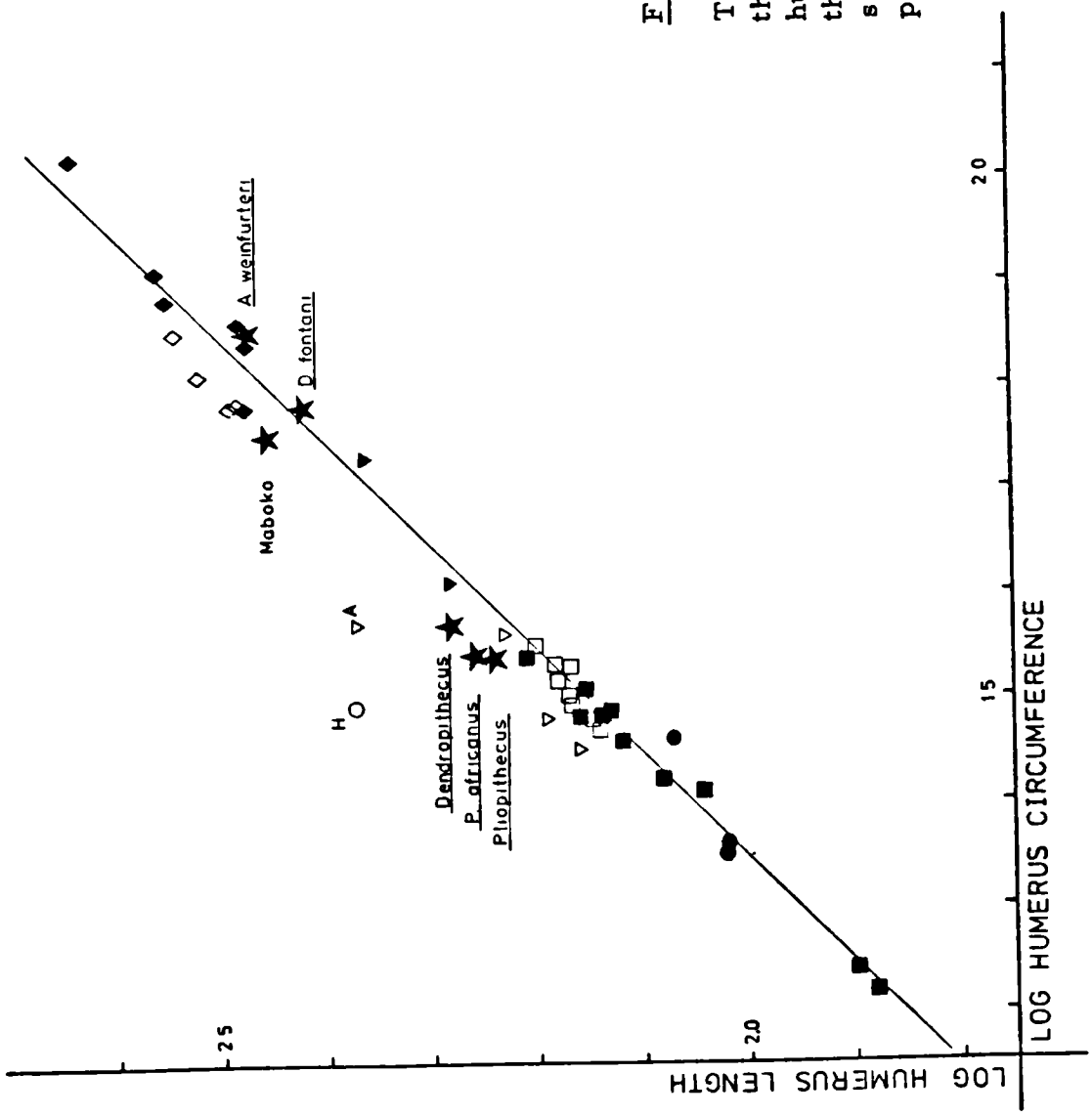

Fig. VII.3.

The relationship between the circumference of the humerus and the length of the humerus including selected fossil higher primates.

Dendropithecus in the relationship between humerus length and humerus circumference suggests a similar conclusion. In addition, the similarity between this fossil primate and Alouatta and Lagothrix in the morphology of the forelimb bones suggests that both the humerus circumference and the humerus length stands in the same relationship to body weight in Proconsul africanus as it does in these primates.

The relatively long humerus in relation to humerus circumference found in these Miocene primates does not necessarily support the hypothesis that these primates are undergoing an elongation of the humerus leading to the extreme specialisation found in the extant Hylobates and Ateles. It has frequently been suggested in the literature (Chapter III) that both Pliopithecus and Dendropithecus may be gibbon ancestors. However, it has never been suggested that Proconsul africanus also shares this phylogenetic relationship. The similarity in the relationship between humerus length and humerus circumference in Proconsul africanus, Dendropithecus and Pliopithecus suggests that a gracile humerus may have been a general feature of forelimb morphology shared between these Miocene forms.

VII. 5. The Relationship Between the Length of the Femur and the Length of the Tibia

Fig. VII.4 illustrates the relationship between femur length and tibia length. The only fossil which has both a femur and tibia which are complete enough for accurate length measurements is Pliopithecus vindobonesis (Ind. III). This specimen

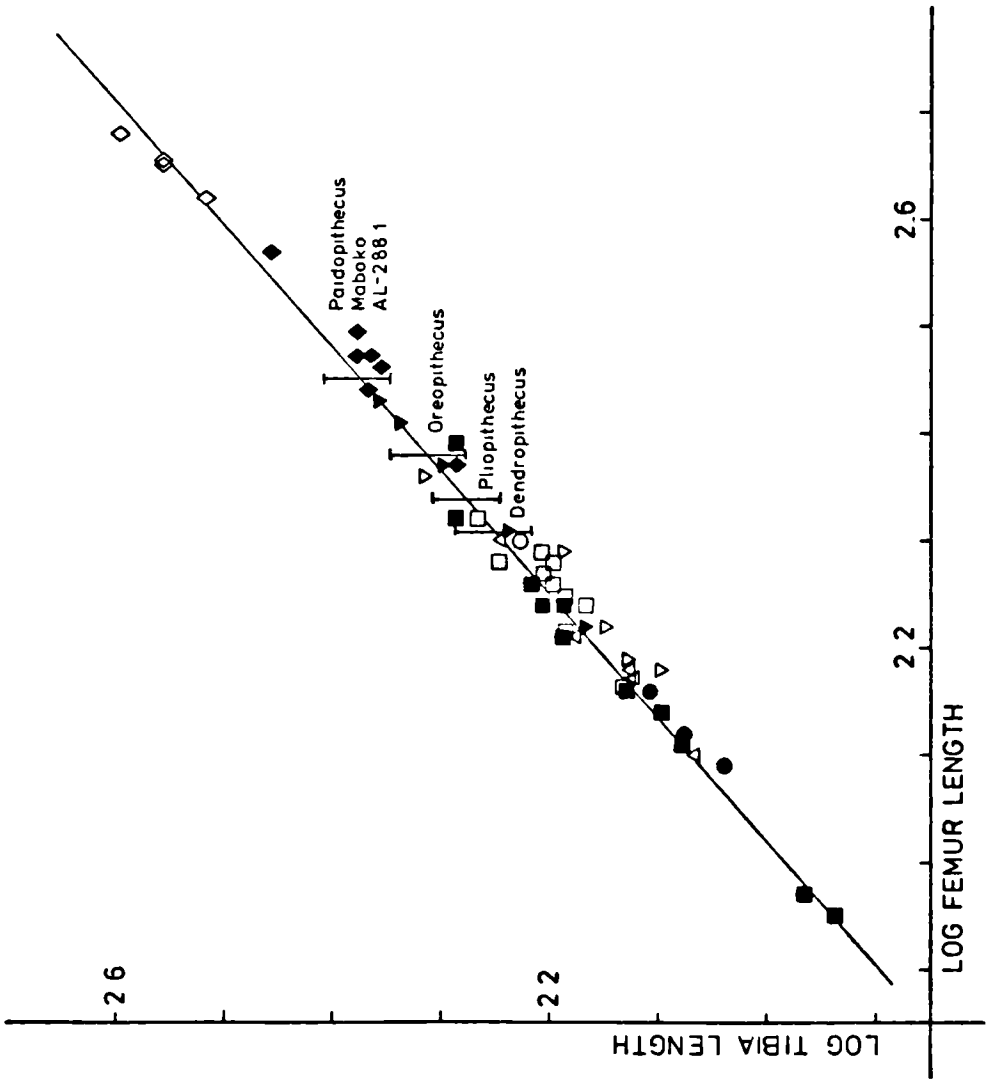

Fig. VII.4.

The relationship between the length of the femur and the length of the tibia including selected fossil higher primates.

clearly falls within the highly correlated Group I and Group II trend.

The high correlation between the length of the femur and the length of the tibia across the Group I and Group II primates (Section V.4) allows the length of one bone to be predicted from the length of the other with a reasonable degree of accuracy. Table VII.1 gives the equations for prediction. Table VII.2 gives the predicted tibia lengths for the fossils which have femur lengths, as well as the predicted hindlimb lengths based on the femur lengths and on the predicted tibia lengths.

VII. 6. The Relationship Between the Length of the Femur and the Length of the Humerus

Fig. VII.5 illustrates the relationship between humerus length and femur length and includes both the fossil primates as well as the available New World primates. The high correlation within the Group I sample (Section V.8) indicates a constant increase in the lengths of these bones relative to each other. The positive principal axis indicates that the femur is increasing in length at a more rapid rate than is the humerus. Mesopithecus is the only fossil which clearly falls within this trend. The remaining fossils deviate from this trend in the direction of a long humerus for their femur lengths relative to the Group I primates. Pliopithecus, Dendropithecus AL-288-1 and KNM-ER-1503/4 all show a relatively uniform deviation from this trend. When the New World primates are taken into consideration, Alouatta and Lagothrix also share this deviant trend, while Cebus lies within the Group I trend. Based on these data, there appears to be two patterns of relationship between femur length and humerus length, the previously described pattern of the Group I primates (Section V.8) and a second pattern shared between Pliopithecus, Dendropithecus KNM-ER-1503/4, AL-288-1, Alouatta and Lagothrix. In this second pattern, the humerus is long relative to the femur, although not exceeding it in absolute length. It is important to emphasise, however, that the lengthening of the humerus in relation to body weight in these primates is not

Table VII.1.

The Prediction of the Length of the Tibia from a Known Femur Length and the Length of the Femur from a Known Tibia Length

X = Log Length of the Femur Y= Log Length of the Tibia

$$Y = .2660 + .8607X$$

95% Confidence Limits: $$Y \pm .0298 \left[1 + \frac{1}{29} + \frac{X - 2.3313}{.9456}\right]^{\frac{1}{2}}$$

$$X = -.2878 + 1.1525Y$$

95% Confidence Limits $$X \pm .0345 \left[1 + \frac{1}{29} + \frac{Y - 2.2725}{.7062}\right]^{\frac{1}{2}}$$

Table VII.2.

	Femur Length	Predicted Tibia Length	95% C.L for Tibia Length	Predicted Hindlimb Length	95% C.L. for Hindlimb Length
Pliopithecus vindobonensis Individual I	217	189.23	176.44 - 202.95	406.23	393.44 - 419.95
Individual II	206	180.95	168.85 - 193.90	386.95	347.85 - 399.90
Paidopithex rehanenus	284	238.54	221.53 - 256.87	522.55	505.53 - 540.87
Proconsul sp. (Maboko)	285	239.27	222.19 - 257.66	524.27	507.19 - 542.66
Dendropithecus macinnesi	214	186.98	174.38 - 200.49	400.98	388.38 - 414.49
Mesopithecus pentelici	167.5	151.43	141.78 - 161.74	318.93	309.28 - 329.24
Oreopithecus bambolii	243	208.59	194.16 - 224.09	451.59	437.16 - 467.09
KNM-ER-1481	395	316.88	292.90 - 342.82	711.88	687.90 - 737.82
AL-288-1	280	235.65	218.88 - 253.70	515.65	498.88 - 533.70

All length measurements are in millimeters.

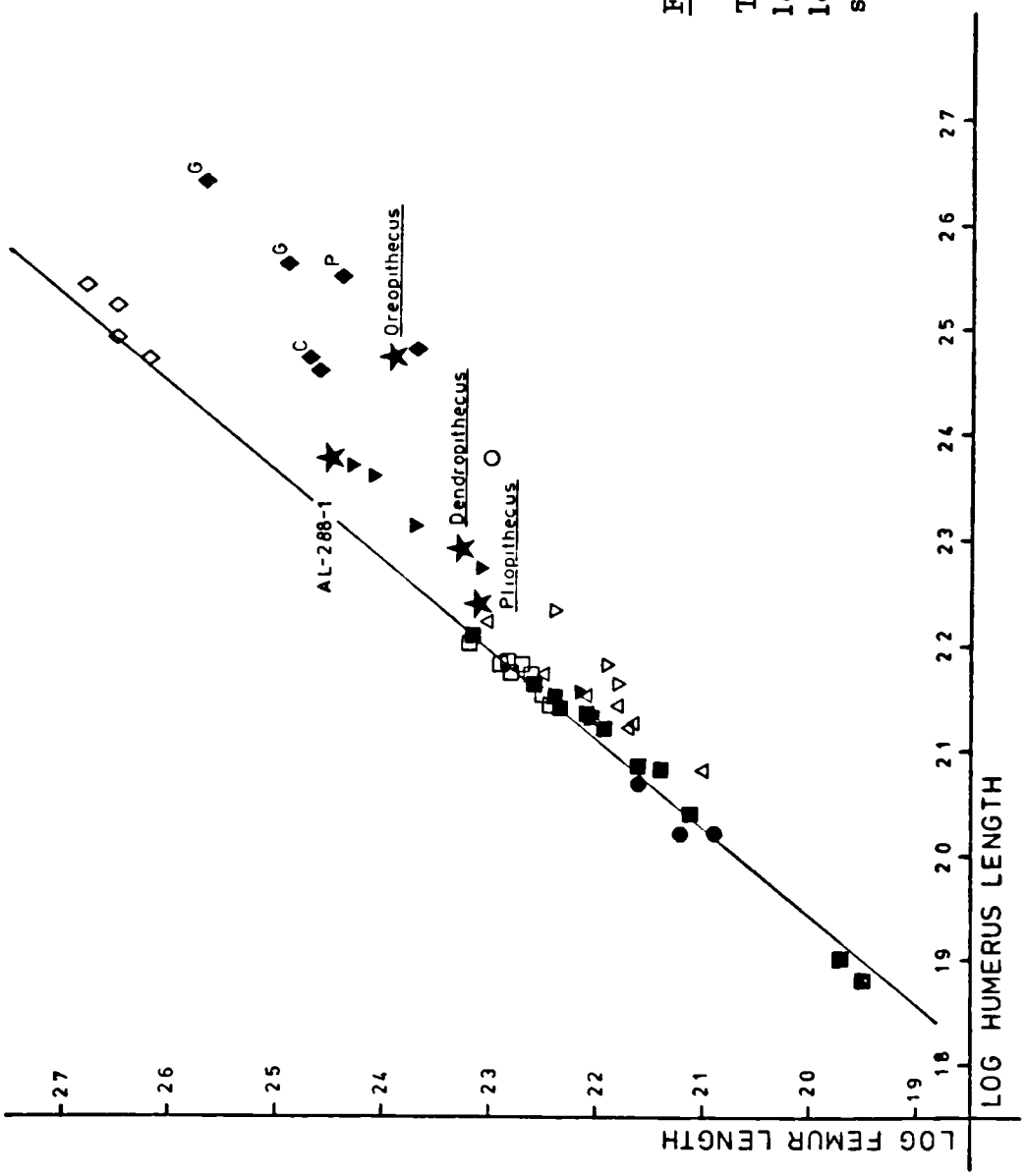

Fig. VII.5.

The relationship between the length of the humerus and the length of the femur including selected fossil higher primates.

of the magnitude of the lengthening seen in Hylobates or Ateles. In addition, the fossil hominids are consistent with the second pattern of proportional relationship shared by Alouatta, Lagothrix, Pliopithecus and Dendropithecus.

VII. 7. The Relationship Between the Length of the Humerus and the Length of the Radius

Fig. VII. 6 illustrates the relationship between humerus length and radius length in the Group I and Group II primates, the fossil primates and the New World primates. Among the fossil primates, Pliopithecus, Dendropithecus and Oreopithecus are consistent with the general Group I trend (Section V.10). The remaining fossils have a relatively short radius in relation to their humerus lengths based on this trend (Cebupithecus, Proconsul africanus, Austriacopithecus weinfurteri). The New World monkeys show a similar dicotomy in the relationship between these two bones. Alouatta and Lagothrix have a short radius for their humerus lengths and Cebus, Brachyteles and Ateles have a long radius in relation to their humerus lengths in general consistency with the Old World monkeys. The sample of New World primates is not large enough to determine the actual principal axis for this group and to test the hypothesis that Cebus, Alouatta and Lagothrix fall on the same trend. However, the South American Miocene fossil, Cebupithecia, argues against a constant New World pattern. It is possible to argue on the basis of the present evidence that Cebupithecia, Alouatta, Lagothrix, Brachyteles and Ateles represent the general trend of the New World primates, while Cebus is specialised with a relatively long radius for its humerus length.

Both Pliopithecus and Dendropithecus have radii which are relatively long in relation to their humeri and both Proconsul africanus and Austriacopithecus weinfurteri have radii which are relatively short. Therefore, among the Miocene apes there are at least two brachial patterns represented.

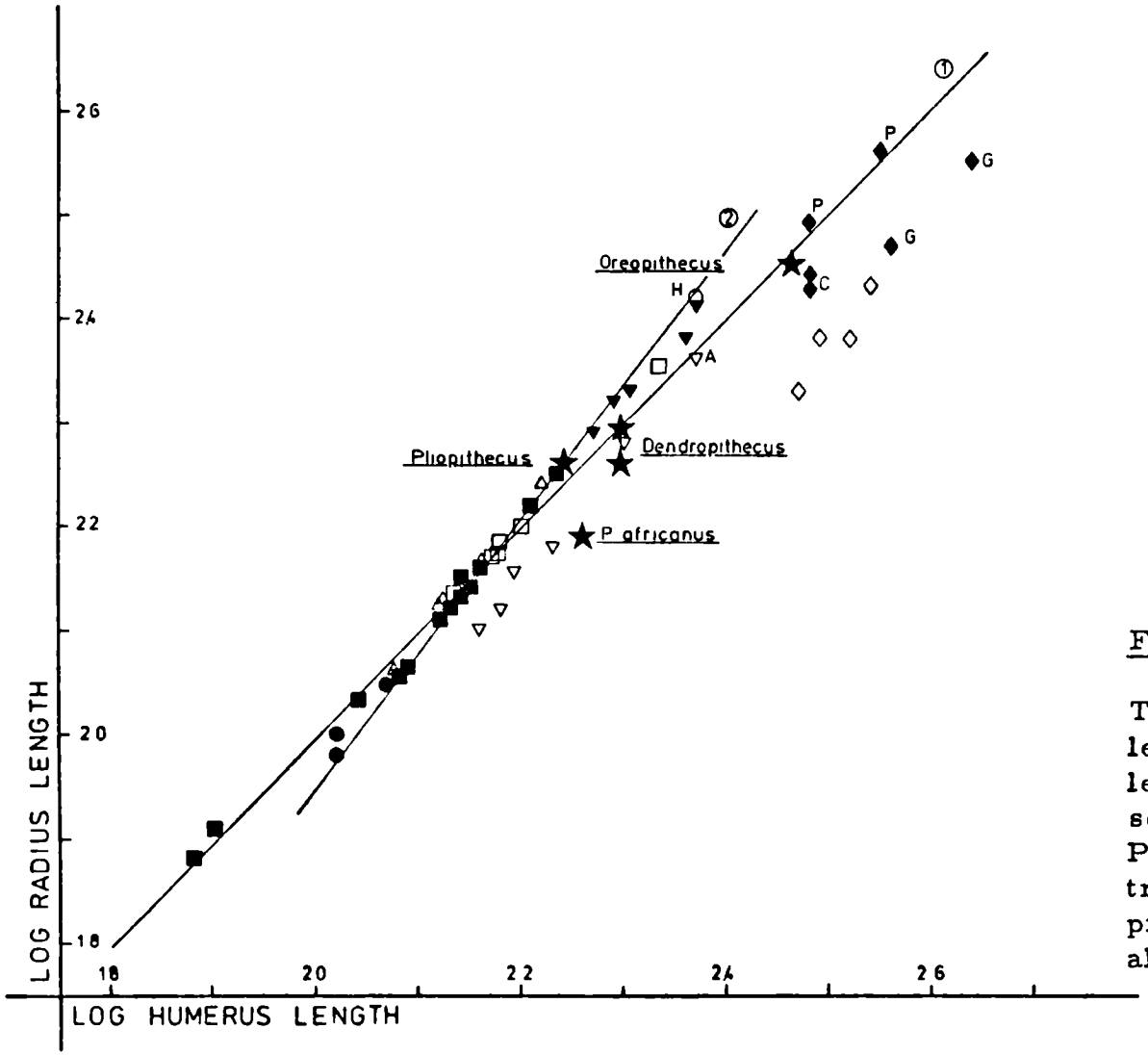

Fig. VII. 6

The relationship between the length of the humerus and the length of the radius including selected fossil higher primates. Principal axis '1' is the isometric trend for this relationship while principal axis '2' is the positive allometric trend.

Among the extant Hominoidea, Gorilla and Homo share relatively short radii in relation to their humerii. Pongo is characterised by a relatively long radius and Pan by a radius of intermediate length. Without more fossils relevant to the ancestry of these extant primates it is difficult to suggest the evolutionary consistency or deviations in the brachial pattern. The long radius in Pongo has obvious biomechanical implications for its arboreal mode of locomotion (Chapter IX). However, lacking fossils relevant to the ancestry of Pongo, it cannot be established whether or not this is a long standing characteristic or a relatively recent development relevant to the current locomotor pattern of this primate. However, the similarity in brachial proportions between Creopithecus and Pongo show that a relatively long radius was present in at least one large bodied Miocene primate.

The situation found in the other extant hominoids is equally difficult to interpret in a phylogenetic context. Both Proconsul africanus and Austriacopithecus weinfurteri deviate from the Group 1 primate trend to a greater extent than does Pan. Austriacopithecus weinfurteri deviates as much as does Homo sapiens (caucasian). However, there is no certainty that the two Austriacopithecus forelimb bones come from the same individual. Because of this, the low brachial index presented here may not be an accurate reflection of the true Austriacopithecus forelimb proportions. Pan does not appear from these data to be only a small version of the proportions seen in the larger Gorilla. This and the locomotor differences between Homo and Gorilla (primates which are similar in their brachial proportions) suggest that the variations observed in brachial proportions are alterations resulting from different locomotor lifestyles and do not have close phylogenetic consistency. The presence in Proconsul africanus of a short radius makes plausible the assumption, however, that extant hominoids could have evolved from a Miocene ancestor, who already possessed a short radius relative to humerus length.

VII. 8. The Relationshp Between the Length of the Tibia and the Length of the Radius

Fig. VII.7 illustrates the relationship between radius length and tibia length and includes both the New World primates and the fossil primates. None of the fossil primates that have radii also have tibia from which accurate length measurements can be made. The estimates of tibia length used in Fig. VII. 7 are derived from the femur length based on the formula in Section VII. 5. The high correlation between femur length and tibia length across the entire sample makes these estimates reasonably reliable. The three fossil primates all lie significantly above the Group 1 trend, indicating longer radii in relation to their tibias than would be expected on the basis of this trend. The estimated tibia lengths for Pliopithecus and Dendropithecus suggest tibias of approximately the same length as their radii. The estimated tibia length for Oreopithecus suggests a much longer radius than tibia. This is consistent with the general proportional similarity of Oreopithecus and Pongo in the comparison between humerus length and femur length (Section VII. 6) and in the comparison between humerus length and radius length (Section VII. 7). As in the great apes, the position of Oreopithecus may result from a shortening of the hindlimb and, therefore, the tibia, in relation to body weight rather than from a lengthening of the forelimb and, therefore, the radius.

In this comparison, the New World primates follow two distinct patterns. Cebus apella and Cebus albifrons follow the Group 1 trend and have tibia longer than their radii. Alouatta and Lagothrix, however, fall above the Group 1 trend and have radii of approximately the same length as their tibias. These species deviate from the Group 1 trend to approximately the degree as do Pliopithecus and Dendropithecus.

VII. 9. The Relationship Between the Length of the Forelimb and the Length of the Hindlimb

Fig. VII.8 illustrates the relationship between hindlimb length and forelimb length and includes the New World primates

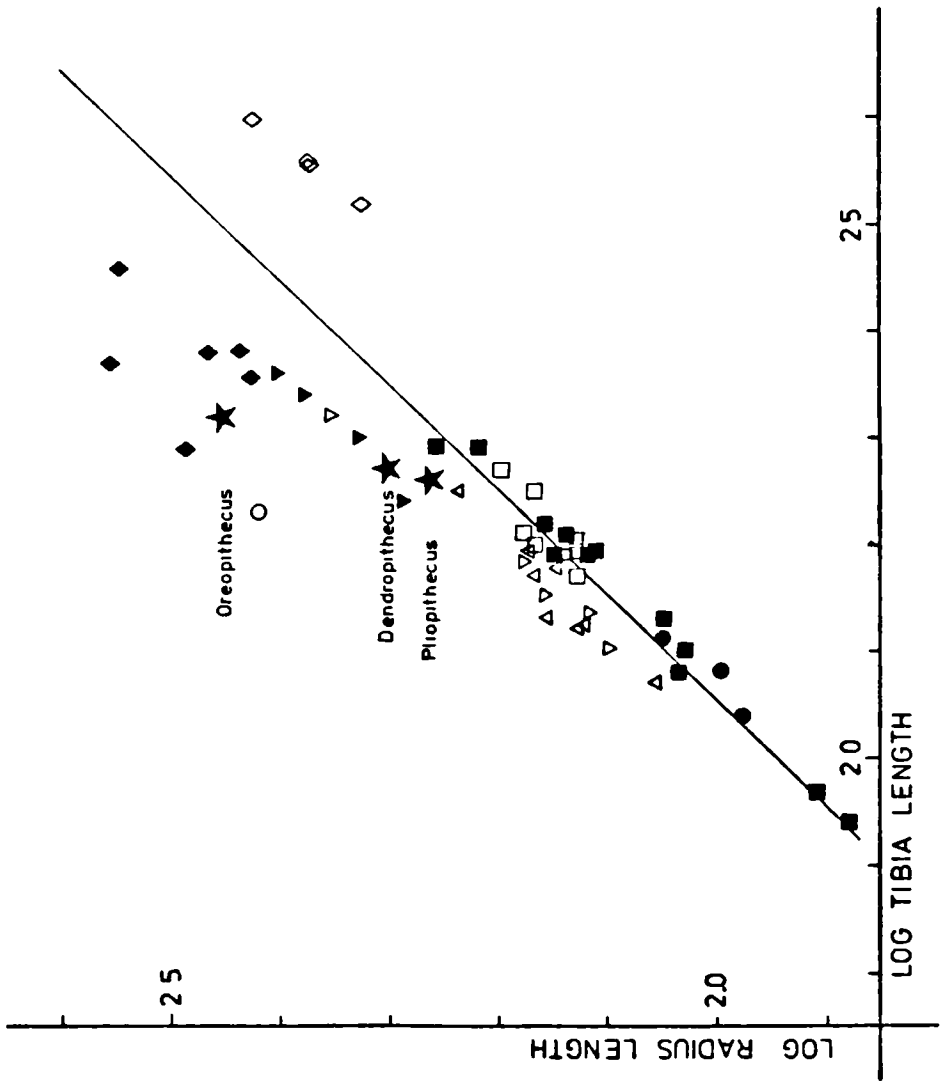

Fig. VII.7.

The relationship between the length of the tibia and the length of the radius including selected fossil higher primates.

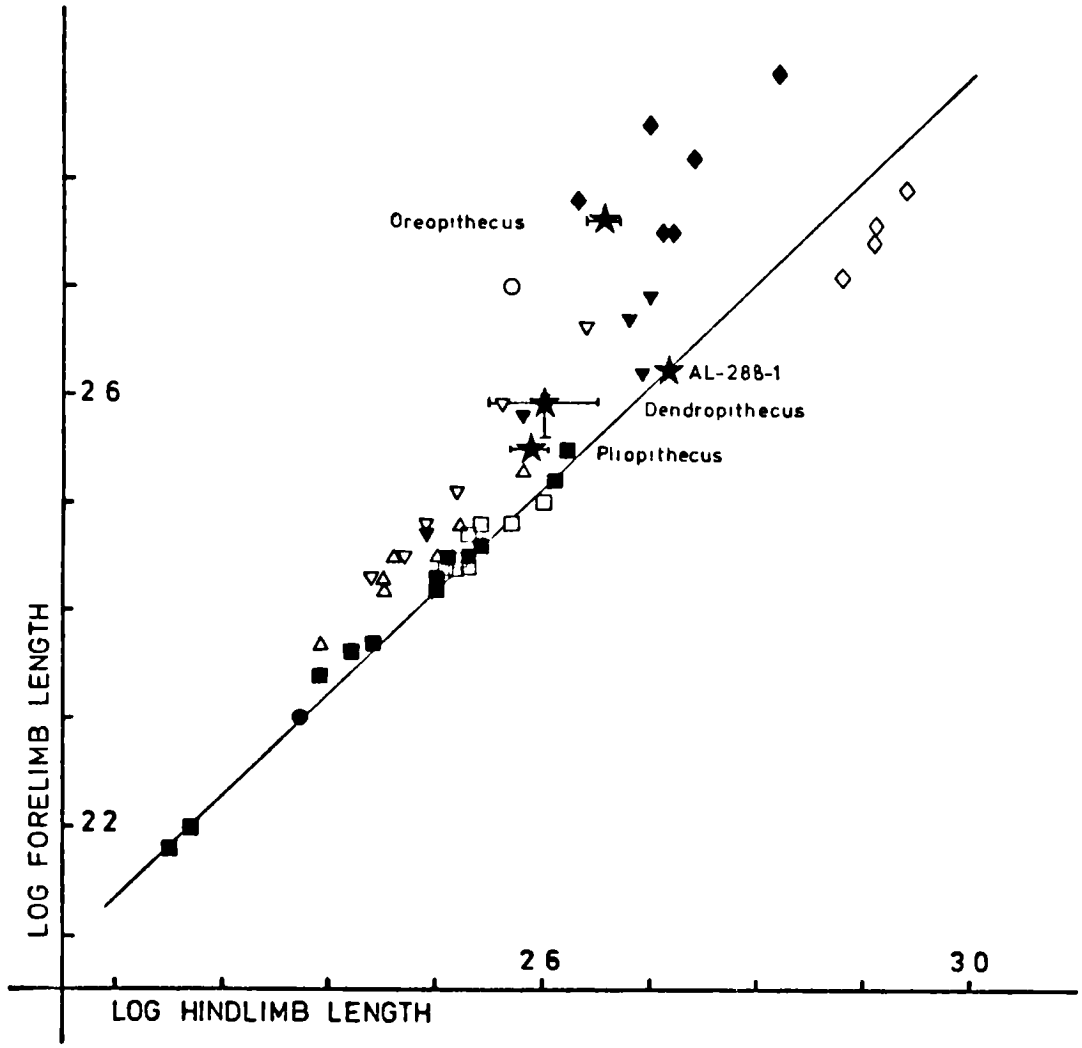

Fig. VII. 8.

The relationship between the length of the hindlimb and the length of the forelimb including selected fossil higher primates. Hindlimb lengths for the fossils are estimates based on the length of the femur (section VII. 5 The forelimb length of Al-288-1 is based on the published length of the humerus and the length of the radius scaled from photographs.

as well as the three fossil species for which the length measurements of the four bones necessary to make up the two limb lengths are available. All of the fossils fall significantly above the Group 1 trend. The Group 1 trend is just not significantly different from isometry (Section V.14), and, therefore, the two limbs increase in length at a constant rate. The hindlimb, however, maintains an absolutely greater length than the forelimb. Pliopithecus and Dendropithecus have significantly longer forelimbs than the Group 1 expectation, however, Pliopithecus has a slightly longer hindlimb than forelimb, and Dendropithecus has a forelimb which equals the hindlimb in length. Oreopithecus has a much longer forelimb than hindlimb.

The New World primates are divided into two groups. Cebus is consistent with the Group 1 trend and has a hindlimb longer than its forelimb. This is consistent with the similarity between Cebus and the Group 1 primates in the relation between humerus length and femur length (Section VII.6) and in the comparison between humerus length and radius length (Section VII.7). Alouatta and Lagothrix deviate from the Group 1 trend and have forelimbs which are roughly equal in length to their hindlimbs. These species also deviate from the Group 1 trend in the other bone length comparisons.

1. The relationship between humerus length and femur length (Section VII.6). The length of the femur is close to the length of the humerus in Alouatta and Lagothrix, while in the Group 1 primates the length of the femur exceeds the length of the humerus.
2. The relationship between humerus length and radius length (Section VII.7). The length of the humerus exceeds the length of the radius in Alouatta and Lagothrix, while in the Group 1 primates the length of the humerus and length of the radius are similar.
3. The relationship between radius length and tibia length (Section VII.8). The length of the radius equals the length of the tibia in Alouatta and Lagothrix, while in the Group 1 primates the length of the tibia exceeds the length of the radius.

Therefore, in these New World primates the equal length of the forelimb and the hindlimb is produced by a lengthening of both the humerus and the radius relative to the expectations of the Group 1 trend. The humerus has experienced a greater lengthening than has the radius.

The similarity in the forelimb and hindlimb proportions between these species and Dendropithecus and Pliopithecus is an artefact of differential lengthening of the bones of the limbs and not a function of similarity in all of the bone proportions.

Although Dendropithecus and Pliopithecus deviate from the Group 1 primates in the comparison between femur length and humerus length (Section VII. 6) and have an elongated humerus in relation to the femur based on this trend, the elongationan is not as extreme as the elongation in Alouatta and Lagothrix. In addition, both Pliopithecus and Dendropithecus are similar to the Group 1 trend in the comparison between humerus length and radius length while Alouatta and Lagothrix deviate from this trend with a shorter than expected radius length for their humerii.

VIII. The Prediction of the Body Weight of Fossil Primates

VIII. The Prediction of Body Weight for Fossil Primates

Allometric analysis of post cranial bones in higher primates has revealed a number of parameters which have a constant relationship with body weight across the sample, including the Group I and Group II primates as well as the New World primates These parameters, therefore, can be used to provide a general indication of body weight for the fossil primates. Those parameters which account for the greatest amount of variance of body weight across the entire sample are the transverse diameter of the midshaft of the femur, the circumference of the midshaft of the humerus and the length of the humerus (Table VIII.1).

The transverse diameter of the midshaft of the femur leaves the least amount of the variance of body weight unexplained and, therefore, can be relied upon to give the most accurate prediction of body weight with the narrowest confidence limits. This is not the case for the sagittal diameter of the midshaft of the femur. This parameter shows a constant relationship with body weight in the higher primates under approximately 20,000 grams in weight, but shows a highly variable relationship with body weight in the hominoids above this body weight. The constancy of the transverse diameter of the midshaft of the femur with body weight across the sample can be explained in the context of its role in weight support of the body. In all primates body weight would impose a transverse bending moment on the shaft of the femur as the result of lateral placement of the femur in relation to the position of the body centre of gravity. In the hominids, where bipedal posture would be expected to increase the magnitude of the body weight supported by the hind limb (femur), the ilio-tibial tract acts to reduce the transverse bending moment on the femur (Pauwels, 1948). This allows for a reduction in the transverse dimension of the femur and for the consistency of *Homo* with the remainder of the higher primates in this comparison.

The remaining parameters, the circumference of the midshaft of the humerus and the humerus length, leave a significantly larger amount of the variance of the body weight unexplained than does the transverse diameter of the midshaft of the femur. Therefore, these parameters are less efficient predictors of body weight than is the transverse diameter of the midshaft of the femur. However, because

Table VIII. 1. Statistics for the prediction of body weight from the transverse diameter of the femur, the circumference of the humerus and the length of the humerus.

Measurement from which the prediction is made (y)	N	r	$s^2_{x \cdot y}$	Least Squares Equation	95% Confidence Limits for Predicted Weight
Transverse diameter of the Midshaft of the Femur	46	.99	.0067	LogBW = 1.19 + 2.55Logy	$\pm(.165)\left[\frac{1}{n} + \frac{1}{46} + \frac{(Logy-1.114)^2}{1.623}\right]^{\frac{1}{2}}$
Circumference of the Midshaft of the Humerus	46	.98	.0106	LogBW = -.27 + 2.73Logy	$\pm(.208)\left[\frac{1}{n} + \frac{1}{46} + \frac{(Logy-1.573)^2}{1.389}\right]^{\frac{1}{2}}$
Humerus Length	46	.98	.0093	LogBW = -1.94 + 2.68Logy	$\pm(.195)\left[\frac{1}{n} + \frac{1}{46} + \frac{(Logy-2.227)^2}{1.450}\right]^{\frac{1}{2}}$

Table VIII. 2. Statistics for the relationship between body weight and the circumference of the humerus and between body weight and the length of the humerus.

	Log Humerus Circumference			Log Humerus Length		
	N	r	$s^2_{x \cdot y}$	N	r	$s^2_{x \cdot y}$
Branch Sitting and Walking/ Old World Semibrachiating	20	.97	.0046	20	.97	.0040
Branch Sitting and Walking/ Old World Semibrachiating/ New World Semibrachiating	25	.92	.0107	25	.94	.0083
All Monkeys	36	.94	.0092	36	.93	.0111
Great Apes and Homo sapiens	10	.80	.0113	10	.94	.0039

The following abbreviations are used in these tables. N = sample size. r = correlation coefficient. $s^2_{x \cdot y}$ = the unexplained variance of the relationship.

these parameters leave only four percent of the variance of the body weight unexplained, they can be used with reasonable confidence to predict body weight for those fossils for which no femora are available.

Both the midshaft circumference of the humerus and the humerus length are highly correlated with body weight in the sample composed of only the Group 1 primates (Table VIII.2), and consequently, leave a small percentage of the body weight unexplained. The amount of variance of body weight left unexplained by these variables increases significantly when the New World primates, the macaques and Papio, are included in the sample. This increase in the unexplained variance results from two factors. Firstly, this increase results from variation in the length of the humerus in relation to both the length of the femur (Fig. VII.5) and to body weight in the New World primates, in Papio and, to a varying extent, in the macaques. Therefore, the length of the humerus varies in these primates at the same body weight. Secondly, there is a high correlation between the midshaft circumference of the humerus and the length of the humerus in these primates ($r = .99$, $s^2 x\,y = .0009$). Therefore, as the length of the humerus increases so does the midshaft circumference of the humerus. Both of these measurements can be expected to slightly overpredict body weight in these primates which for locomotor reasons have a long humerus for their body weights, and to slightly underpredict body weight for those which do not.

In additon, the length of the humerus is exceedingly long in relation to both humerus circumference (Fig. VI.19) and to body weight (Fig. V.6) in the gibbons and in Ateles, although the circumference of the midshaft of the femur is not correspondingly large. Therefore, there is the possibility of seriously over estimating body weight in fossil primates of unknown locomotor pattern if the humerus length is the sole measurement used for prediction. This possibility is minimised, however, if the humerus length is compared to humerus circumference as in Fig. VI.19 before the prediction is made. Over prediction of body weight is not a danger in the larger size ranges, however. Humerus length leaves a significantly smaller amount of the variance of body weight unexplained in the great apes and human beings than it does in the combined monkey sample (Table VIII.2). Therefore, humerus length can be relied upon to give an accurate prediction of body weight in the

larger size ranges. This is not true of the humerus circumference in these primates, however. The humerus circumference of Homo sapiens is considerably smaller in relation to body weight than it is in the great apers. This is reflected in the relatively high unexplained variance of body weight by this measurement in these primates and is most likely related to the non-locomotor function of the forelimb in human beings

Table VIII. 3 gives the predicted weights for Miocene and selected Plio-Pleistocene hominoids based on these measurements. For Pliopithecus and Dendropithecus the transverse diameter of the midshaft of the femur most likely represents the accurate weight. Both of these hominoids are characterised by a long humerus in relation to their femur lengths (Fig. VII. 5). The weight of Proconsul africanus, for which there is no femur, is probably best represented by the humerus circumference measurement. In the comparison between the circumference of the midshaft of the humerus and the length of the humerus (Fig. VI.19) it is similar to both Pliopithecus and Dendropithecus, and it is likely that the length of the humerus overpredicts body weight for Proconsul africanus as it does in these primates. The remainder of the weight predictions are unambiguous and can be considered the best estimates of body weight for these primates.

Table VIII. 3. Predicted body weights for selected Miocene and Plio Pleistocene hominoids.

	Log Body Weight -- Predicted Means and 95% Confidence Limits	N	$\bar{x}$ (mm)	Weight (grams)	95% C.L. for Weight	Parameter
Pliopithecus vindobonensis		2	11.60	8023	6034 - 10457	FTD
		1	33.5	7823	4823 - 12961	HC
		1	173	11428	7259 - 17991	HL
Dendropithecus macinnesi		3	11.07	7121	5642 - 8884	FTD
		1	37.25	10452	6446 - 16947	HC
		1	193	15321	9728 - 24131	HL
Proconsul africanus		1	34.7	8612	5310 - 13967	HC
		1	182	13092	8316 - 20611	HL
P. rehenanus		1	16.00	18218	12397 - 26775	FTD
Proconsul sp.		1	16.60	20011	13611 - 29421	FTD
D. fontani		1	265	35834	22761 - 56416	HL
Austriacopithecus weinfurteri		1	70.00	58195	35628 - 96029	HC
		1	300	49967	31441 - 79408	HL
O. kamboli		1	297	48639	30620 - 77272	HL
Al - 288 - 1		1	235	25969	16482 - 41013	HL
KNM-ER-1481		1	25.3	58308	39537 - 86896	FTD
KNM-ER-739		1	328	63460	39811 - 101158	HL
	4.0 4.5 5.0					

Table VIII. 3.

Predicted body weights for the fossil primates based on the transverse diameter of the midshaft of the femur (FTD), length of the humerus (HL), and circumference of the midshaft of the humerus (HC). N = the number of fossil specimens upon which the body weight prediction is based. x = the absolute measurement in millimeters upon which the prediction of body weight is made. Measurements of the fossil specimens are taken from the literature indicated in Table III. 3.

IX. The Allometry of Primate Limb Proportions

IX 1. Introduction

Allometry (scaling of characteristics to body size) has shown a recent revival in the analysis of morphological specialisation, as well as in other areas of analysis where size is an important correlate of the variable under study (Gould, 1966, 1975, Pilbeam and Gould, 1974, Jerison, 1973, Sacher, 1970). Change in shape of a morphological element may occur as a correlate of change in size of an animal or as the result of a particular specialisation independent of body size. It is desirable, to both taxonomic and functional analyses to separate the effects of these two variables.

Since the middle of the 19th century, the necessity of correcting limb and bone length for the effects of body size in comparative analyses has been recognised (Huxley, 1864, Lucae, 1865, Mivart, 1867). However, until recently in the analysis of the primate post crania this has been achieved through the use of indices composed of either a measure of body size and limb or bone length or of two limb or bone lengths. These early analyses as well as subsequent work (Mollison, 1910, Schultz, 1930, 1933, 1937, Erikson, 1963) have provided a body of data which outlines the general proportional relationships in higher primates.

However, indices are not an ideal means of either correcting for the effects of body size or analysing the relationship between body size and limb or bone length. If the two variables comprising the index do not change in length at the same rate, or isometrically, in primates of different sizes radically different indices can result. This can occur even though there may be a constant and highly correlated allometric relationship between the variables comprising the index. This problem is accentuated if one of the variables comprising the index is body weight while the other is limb or bone length. Body weight is proportional to body volume, which would increase in approximate proportion to the cube of a linear measurement. Therefore, even if there were geometric similarity (identity in proportions)

in primates of different sizes, indices would obscure this homogenity.

Allometry as a technique which employs logarithmic transformation to correct for differential increase between variables and bivariate plots to illustrate constant proportional relationships, avoids the pitfalls of indices. The resulting bivariate display separates those specimens which show a constant linear relationship with body weight from those specimens which deviate from the linear relationship. The interpretations based on these allometric relationships are dependent on the assumptions made in the construction of the bivariate plot and on the statistical interpretation of the observed relationships. There are a number of specific factors which influence the interpretation of the allometric relationships. These include the nature of the sample employed as the basis of analysis, the validity of the statistical techniques used to characterise the relationships, the significance attributed to the variation around the linear trend and the validity of the relationship between the actual metrical parameters used in the analysis and the specific dependent or independent variables they are assumed to represent.

Of these factors, attention in the literature has been directed primarily toward the validity of alternative statistical techniques available for the characterisation of the observed linear relationships. Least squares regression analysis is the most frequently used technique for this purpose. However, it takes into consideration variation in only one of the variables in the analysis and, as a result, it can produce misleading results when the correlation coefficient is low. Statistical techniques, such as reduced major axis and principal axis, which take into consideration variation in both parameters, are becoming increasingly popular as techniques which provide an accurate characterisation of the linear relationship. However for interspecific analyses, which normally produce correlation coefficients in excess of 95, the results of these

various statistical techniques are seldom significantly different.

Little attention has been drawn to the remaining factors involved in the interpretation of allometric relationships, the nature of the sample used as the basis of analysis, the significance of the variation observed in the relationships and the assumptions surrounding both the dependent and the independent variables. It is the specific purpose of this discussion to examine these factors in relation to the analysis of the allometry of the adult primate post cranial skeleton.

IX 2. Body Weight and Skeletal Trunk Length as Measures of Body Size in the Higher Primates

In the analysis of the allometry of limb bones in the Anthropoidea, the skeletal trunk length (Rumpfskelettlänge of Mauer, 1970/71, Biegert and Mauer, 1972, and Halaczek, 1972) has most frequently been used as the standard of body size. However, as Chapter IV has shown, the skeletal trunk length is not a constant measure of body weight across the entire sample of higher primates. Papio and the Hominoidea fall significantly below the principal axis characterising the remaining higher primates and, therefore, have skeletal trunk lengths which are significantly short in relation to their body weights. This inconsistent relationship between skeletal trunk length and body weight has seriously affected the interpretation of limb proportions in the higher primates.

1. Cross-sectional measurements. Using skeletal trunk length as the standard of body size, Halaczek (1972) has shown that there are two allometric trends within the higher primates for the circumference of the femur midshaft, the circumference of the head of the femur, width of the medial and lateral epicondyle of the femur, width of the proximal piphysis of the tibia and width of the distal epiphysis of the tibia. It is significant that the species composing the two allometric trends in these comparisons are those species which also compose the two trends in the comparison between the skeletal trunk length and

body weight in Chapter V. In Halaczek's comparisons the Hominoidea and Papio (particularly in the comparison between femur midshaft circumference and skeletal trunk length) consistently fall above the trend formed by the remaining Group 1 primates. As Chapter VI illustrates, these two trends merge into one when femur midshaft circumference is compared to body weight. This suggests that, at least in this comparison, Halaczek's two trends are actually reflecting differences in skeletal trunk length between these two species rather than differences in femur midshaft circumference.

2. Limb Length. Using skeletal trunk length as the standard of body size, Mauer (1970/71) and Biegert and Mauer (1972) have concluded that there is a positive allometry of both the forelimb and the hindlimb in relation to skeletal trunk length within the higher primates. In addition, they have concluded that there is a greater positive allometry of the forelimb in relation to skeletal trunk length than of the hindlimb in relation to skeletal trunk length. This interpretation suggests that, by virtue of body size alone, the limb proportions of the apes could be derived from the proportions of the monkeys. Therefore, the longer legs of Homo represent a specialised condition in relation to this trend. This conclusion is fundamentally altered when body weight is used as the standard of body size. In the Group 1 primates both the length of the forelimb and the length of the hindlimb are isometric with body weight and the relationship of a longer hindlimb than forelimb is maintained throughout the size range of the group (Sections V.6, V. 13, V.14). The forelimb of the Hominoidea is consistent with this trend and is isometric with body weight. The hindlimb of the apes lies significantly below the isometric trend characteristic of the Group 1 primates,

and represents a specialised condition of a shortened hindlimb in relation to this trend, while the hindlimb of Homo falls close to an extension of the Group 1 trend. This interpretation is independently supported by the comparison of the length of the forelimb to the length of the hindlimb Section V. 14). In this comparison, the length of the forelimb and the length of the hindlimb in the Group 1 primates are clearly isoemtric, and, therefore, show no evidence of the positive allometry of the forelimb in relation to the hindlimb, which is suggested by Mauer (1970/71) and Biegert and Mauer (1972). The Pongidae are clearly deviant in the direction of a longer forelimb for their hindlimb length, which directly reflects the relationship suggested by the comparison between body weight and forelimb and hindlimb length. Homo sapiens deviates in this comparison in the direction of a longer hindlimb for its forelimb length. This does not invalidate the conclusions drawn from the comparison between body weight and forelimb and hindlimb length, but rather illustrates the difficulties in extrapolation based on animals of a relatively small body weight to isolated species of a relatively large body weight. This underlines the necessity of testing any hypotheses concerning the primitive or derived nature of such features against the maximun amount of information relevant to the comparison. In this specific case such relevant information would include not only the allometric relationships of the individual bones to each other and to body weight, but also the discrete morphological features of the limb bones. Therefore, body weight, and not skeletal trunk length, when used as a standard of body size in allometric comparisons of limb length, results in conclusions which are consistent with those derived from the direct comparisons of limb or bone lengths with each other.

This is not to say that the relationship between trunk length and limb or bone length is not interesting, but only that the questions asnwered by this type of comparison are not questions of the relationship of limb or bone length to body size, but questions of the relationship of limb or bone length to trunk length, which, in iteself, has a variable relationship with body weight.

IX 3. The Allometry of the Post Cranial Skeleton in the Higher Primates

Allometry is an effective means by which to recognise the relationship of body size to a particular post cranial variable. However, the previous section has demonstrated that the two parameters which have been used to measure body size in analyses of the primate post cranial skeleton do not have a constant relationship with each other across the higher primate sample. This fact underlines the necessity of clearly outlining the assumptions which are made in the interpretation of the allometric relationship between body size (whether measured by skeletal trunk length or by body weight) and the particular variable under analysis. These assumptions are different depending on the nature of the dependent variable under analysis. Variables of bone or limb length stand in a different relationship to body size than do variables of bone cross-sectional size or strength.

IX 4. The Siginficance of the Allometry of Limb Length and Bone Length in Higher Primates

Differences in body proportions or limb proportions between adult primates result from the differential growth of the body segments during the ontogeny of the animal. There are three factors which affect proportions in the adult animal, the speed of growth of the segments in relation to each other, the time of onset of growth in the different segments and the total duration of growth (Gould, 1977, Lumer, 1939, Lumer and Schultz, 1947).

Ontogenetic studies of the limb growth in primates

suggest that differences in limb proportions within species or between some closely related species result from differences in the duration of growth while maintaining the same growth curve, i.e. a constant relationship of speed and onset of growth between segments. Lumer (1939) and Lumer and Schultz (1947) have shown that this is true for different species of Hylobates, as well as being generally true for Macaca. In addition, sexual differences in proportions between males and females of Gorilla, Pan, Ateles and Macaca have been shown to result from this factor (Lumer, 1939, Lumer and Schultz, 1947), while differences in proportions between genera Gorilla, Pan and Pongo result from differences in the speed and onset of growth of the different segments as well as from differences in the total duration of the growth period (Lumer, 1939, Lumer and Schultz, 1941).

These results indicate that it is not the differences or similarities in body proportions, but the ontogenetic causes of these differences or similarities which are important in establishing morphological affinity. As a result, hypotheses which are orientated toward interspecific similarity or difference in growth factors are best tested by ontogenetic analyses of proportional growth.

Static allometric analyses of adult animals are, on the whole, unsuitable for this type of interpretation. In order for them to be useful in this context, the independent variable in the analysis must have a known and constant relationship to growth across the entire sample. For example, age at skeletal maturity would be a factor which would consistently reflect the duration of the growth process resulting in the adult skeletal proportions. Linear relationships resulting from the application of this factor as the independent variable in allometric analysis, would then reflect a common ontogenetic growth curve resulting from similar speeds of growth and time of onset of growth. Deviations from the linear relationship would result from essential differences in the ontogenetic curve resulting from differences in these factors.

Age at skeletal maturity is an unknown factor for many primate species and, therefore, there are no comprehensive data for such an analysis. The traditional variables of trunk length and body weight cannot, at present, be accepted as reflections of constant growth relationships across the sample. In relation to trunk length, both the proportions of the individual vertebrae and the proportions of the vertebral column as a whole reflect locomotor specialisations across the higher primates (Rose, 1975). These differences in vertebral proportions can be expected to have resulted from the same ontogenetic factors which produce variations in limb proportions across the sample. Total trunk length cannot, therefore, be accepted as a reflection of constant growth across the sample

Body weight is a measure of total growth in an organism. As such it measures the result of not only skeletal growth but also growth in soft tissues. Consistent linear allometric relationships of skeletal proportions and body weight, therefore, reflect not only consistency in the particular skeletal parameter under consideration, but also consistency in the total skeletal and soft tissue composition of the body. It is not clear how variations in total skeletal and soft tissue composition affects the allometric relationship between body weight and a particular skeletal variable, such as hindlimb length or forelimb length. The lack of clear statistical separation in the relationship between body weight and either forelimb or hindlimb length between those smaller bodied primates distinguished by differences in intermembral proportions most likely results from this factor.

The relationship between variation in total skeletal and soft tissue composition, body weight and a particular skeletal variable is also significant in the interpretation of the allometric relationship between primates of grossly different body sizes. For example, in the relationship between body weight and hindlimb length, Homo sapiens is consistent with the allometric trend characterising the smaller bodied higher primates. The great apes deviate from this trend in the direction of a short hindlimb

for their body weight. There are gross differences in the distribution of body weight in man and in the great apes. Until the relationship between body weight and growth of the skeleton is established, the question of the apparent similarity in body proportions between man and the smaller bodied primates cannot be firmly accepted as an indication of a shared growth relationship. This similarity could equally well result from convergence of proportions due to different relationships between the duration of growth and the speed and onset of growth in different segments.

Therefore, body weight is not an ideal independent variable in allometric analyses where questions of similarity or difference in the growth process producing the adult proportions are of interest. At best, these analyses can give general indications of proportional similarity or difference, but not the causes of these similarities or differences.

However, the direct comparison of the length of two bones or the length of two limbs, or skeletal trunk length and the length of a bone or a limb can be helpful in this type of analysis. These bivariate comparisons cannot strictly be termed allometric because they do not involve body size as an independent variable. However, the comparison of two skeletal lengths records the results of the ontogenetic process without the complications introduced by the composite measurement of body weight. As a result, the linear trends produced by these comparisons are clearer, the correlation coefficients higher, and the distinction between primates of different locomotor groupings more apparent than those involving body weight as an independent variable.

IX 5. <u>The Relationship Between Allometry and Locomotor Pattern in the Higher Primates</u>

The previous section has shown that allometry of primate body weight and limb and bone length as well as the direct comparison of limb length or bone length with each other are best suited for ordering species for locomotor or mechanical analysis. Because body weight does not have a known constant

relationship to any of the ontogenetic factors producing adult body proportions, interspecific allometric analysis involving adult body weight is not suitable in itself to provide answers to questions of similarity or difference in the growth factors producing adult limb proportions. In the following discussions a size related locomotor classification of the primates is presented and the allometry of primate body proportion is discussed in relation to this classification.

IX 6. Size Related Locomotor Patterns in Extant Higher Primates

Modern higher primates are characterised both by a wide range of body sizes and by a diversity of locomotor behaviours. Weights of extant higher primates range from approximately 100 grams in the small bodied Callitrichidae to approximately 140,000 grams in the largest primate, the male Gorilla (Table III.2) Rose (1973a, 1973b) and Ripley (1979) have emphasised the effect of body size on primate positional behaviour. As the body size increases the branch to body weight ratio decreases and problems of balance in arboreal locomotion become critical. Rose (1973b) suggests a locomotor classification of quadrupedal primates based both on body weight and positional behaviour which illustrates the specialisation in quadrupedal locomotion in large bodied primates not seen in smaller bodied forms (Table III.2) While he recognises only two categories of locomotion in the small and medium primates (ca. 136 - 3820 grams), he recognises five distinct categories of locomotion in the large size range (ca. 2500 - 140,000 grams). These categories are Branch Sitting and Walking, Old World Semibrachiation, New World Semi-brachiation, Ground Standing and Walking, and Knucklewalking. In addition, Rose recognises a sixth locomotor category which combines the locomotor behaviour of two of these distinct categories, Part Branch Sitting and Walking and Part Ground Standing and Walking. The two categories of locomotion in the small and medium size ranges grade into one another. The Small Size Arboreal Quadrupeds include the New World Callitrichidae (136 - 595 grams), while the Medium Size Arboreal Quadrupeds include the New World Cebidae (603 - 3820 grams).

The locomotor behaviour of some of the smaller Cebidae resembles that of the small size Callitrichidae, while the locomotor behaviour of some of the larger Cebidae resembles that of some of the primates in the diverse large size locomotor categories. In the large size range five of the six locomotor categories overlap considerably in their weight ranges. Only the Knucklewalking great apes (Pan and Gorilla) are separated from the remaining five categories by a weight hiatus. Rose roughly divides the five overlapping categories into those which emphasise below branch feeding activities employing forelimb suspension and those which do not (either above branch feeding or terrestrial feeding). The category traditionally defined as the New World Semibrachiators (including Alouatta, Lagothrix and Ateles) primarily specialise in below branch activities and engage in a variety of suspended postures when feeding and resting (Rose, 1973b, Ripley, 1979). If the lesser apes are included as a separate category of Brachiators (Fleagle, 1976), they overlap with the New World Semibrachiators in their weight range and can be considered a second category of below branch feeders (Table 111.2). The remaining four locomotor categories are primarily specialised in terms of above branch activities or level surface terrestrial activities. When below branch feeding occurs it takes the form of hindlimb suspension and bimanual harvesting and feeding (Macaca sinica, Ripley, 1979). Suspended postures involving the forelimbs are not common in feeding and resting postures and occur primarily in association with leaping and climbing in locomotion (Ripley, 1979).

The larger size ranges in this group are found in the Ground Standing and Walking and Part Ground Standing and Walking and Part Branch Sitting and Walking species of Papio and Macaca with the exception of the large male Nasalis (ca. 20,000 grams). None of the Branch Sitting and Walking species have both male and female weights which exceed 10,000 grams and only one of the Part Branch Sitting and Walking and Part Ground Standing and Walking primates exceed this weight (Mandrillus sphinx). While among the exclusively Ground Standing and Walking species five of the seven species for which

weight data are available exceed 10,000 grams for both male and female weight means. These data indicate that as size increases in primates which do not employ forelimb climbing behaviour there is a tendency toward more fully terrestrial adaptations.

Although it is instructive to note that there are no below branch feeding primates over 12,000 grams in weight, this does not necessarily suggest that there are any mechanical reasons for this absence. Fleagle (1976) reports that, although the data are poor, both Pongo and Pan have been reported to use suspensory postures involving the forelimbs in feeding behaviour. The absence of smaller bodied Old World below branch feeders may be the result of ecological competition during the course of the hominoid evolution (Andrews, in press). In the New World the below branch feeders represent the largest of the primate species and there is an absence of similar sized above branch feeders. Ripley (1979) suggested that this might result from differences in general forest ecology between New and Old World tropical forests and, particularly, that the 'grain' of the New World forests is not coarsened sufficiently to provide suitable niches for the specialised above and below branch feeders found in the Old World. The absence of terrestrial primates and large bodied primates from both the extant and fossil records must also be viewed from the larger ecological context

IX 7. The Relationship Between Primate Limb Length, Bone Length and Locomotor Classification

The previous section has outlined ten different locomotor categories for the higher primates (Fig. III.1). The seven categories characterising non-human primates above 2500 grams in weight can be divided into two major groupings. The Branch Sitting and Walking primates, the Old World Semibrachiating primates, the Part Ground Standing and Walking and Part Branch Sitting and Walking primates and the Ground Standing and Walking Primates emphasise above branch or level surface feeding activities. The remaining groups, the New World Semibrachiating

Primates, the Brachiators and the Great Apes all incorporate at least some degree of below branch feeding in their locomotor behaviour.

Limb proportions are also valuable in discriminating above and below branch adaptations in extant higher primates. Limb proportions have been discussed in the primate literature since the early work of Huxley (1864), Lucae (1865), Mivart (1867) and Mollison (1910). However, their value in discriminating locomotor function has been limited by confusion over the significance of indices as well as over the absence of detailed locomotor knowledge from the wild. However, the bivariate plot of the intermembral index against the brachial index and of the humero-femoral index against the brachial index clearly differentiates between the below branch feeders and the remaining locomotor categories (Fig. IX.1). The below branch feeders, and particularly the New World Semibrachiators, are characterised by low brachial indices for their intermembral indices and humero-femoral indices. The remaining non-hominoid primates, without exception, are characterised by high brachial indices for their intermembral indices and humero-femoral indices.

When these indices are examined in greater detail it is apparent that both allometry and variation in bone length due to locomotor function contribute to the variation in indices characterising the non-below branch feeders. However, locomotor function is the only factor contributing to the separation between the above branch feeders and the below branch feeders.

IX 8. Above Branch and Level Surface Feeders

In reference to the humero-femoral index, the bivariate plot of the length of the femur against the length of the humerus (Figs. V.7 and VII.5) clearly distingu ishes those primates which share the same proportional relationships between these bones and those which deviate. The Branch Sitting and Walking primates as well as the Old World Semibrachiators, show a constant and highly correlated relationship between these bones throughout their size range. The femur increases at a significantly faster rate than does the humerus, and, therefore, as the femur

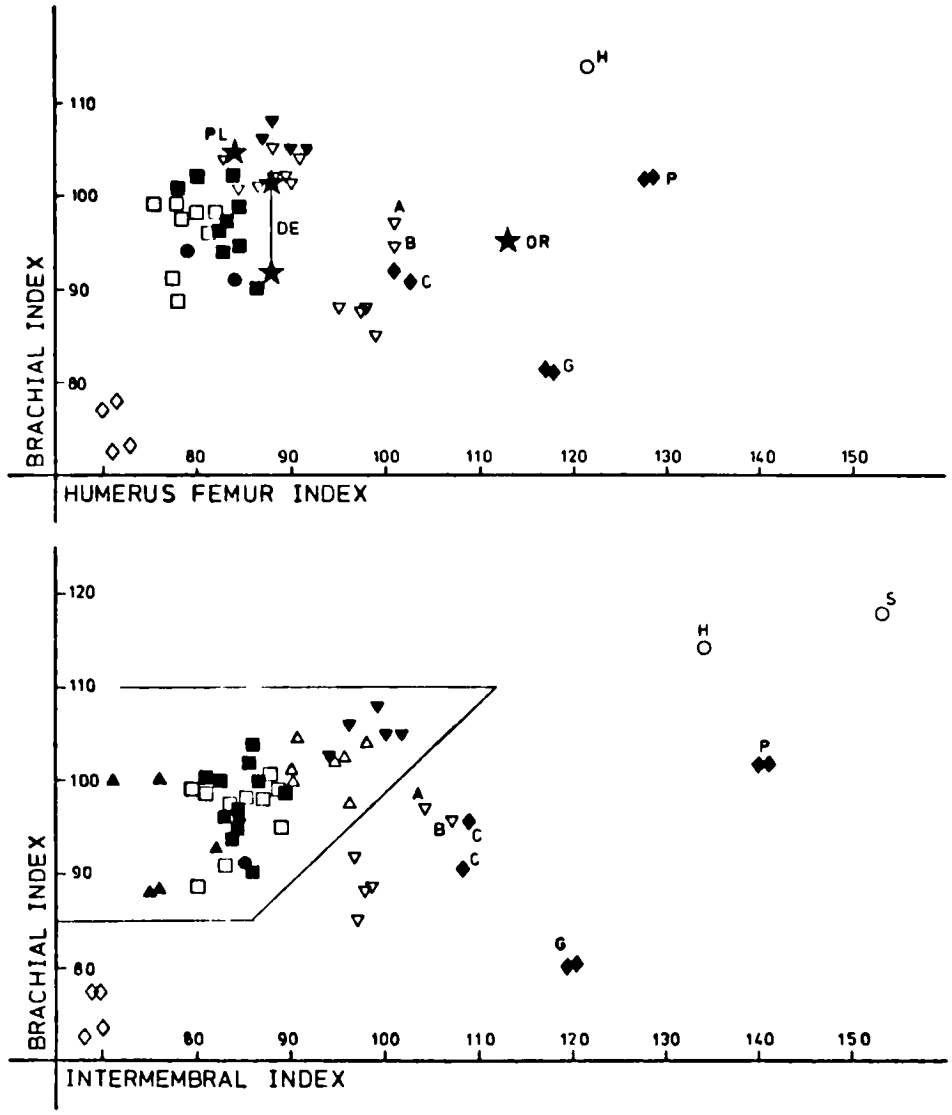

Fig. IX.1.

The relationship between the brachial index and the intermembral index and between the brachial index and the humers-femoral index.

lengthens the humeruo-femoral index decreases. The Ground Standing and Walking primates are displaced significantly from this trend in the direction of a longer humerus for their femur lengths. The Part Branch Sitting and Walking and Part Ground Standing and Walking primates form a variable group, whose limits are defined by the Branch Sitting and Walking primates on the one hand, and by the Ground Standing and Walking primates on the other. Therefore, the length of the humerus relative to the length of the femur appears to correlate with substrate preference of the particular primates species. Those primates such as the Branch Sitting and Walking primates and the Old World Semi-Brachiating primates, which are primarily arboreal in their locomotor pattern, are characterised by a short humerus in relation to their femurs. With increasing terrestriality in the remaining above branch level surface feeders the humerus lengthens in a non-allometric fashion in relation to the femur.

In relation to the brachial index, the bivariate of the plot of the length of the humerus against the length of the radius (Fig. VI.10 and VII.6) shows a highly correlated trend in all of the above branch feeding primates, including the Ground Standing and Walking primates and the Part Ground Standing and Walking and Part Branch Sitting and Walking primates. The length of the radius, therefore, appears to be linked to the length of the humerus in an allometric fashion in the above branch feeders, in spite of the non-allometric alterations in the length of the humerus, which correlates with locomotor function in these primates.

Therefore, the difference in proportion of the forelimbs in relation to the hindlimbs within the above branch/terrestrial feeders have been produced by an alteration of the total length of the forelimb in relation to the hindlimb, and not a basic alteration of the brachial pattern. This would suggest that the brachial proportions themselves are unimportant in the variety of locomotor patterns found in these primates and that the important feature is the total forelimb length in relation to the total hindlimb length. These lengths correlate with the degree of terrestriality or aborealism characteristic of the different species. A short forelimb in relation to the hindlimb is

characteristic of all of the arboreal genera, while a forelimb and hindlimb of equal length is characteristic of the more terrestrial species. The variation in the limb length relationships of Macaca in this context could be taken to reflect the varying terrestrial or arboreal orientation of these primates.

The relatively long length of the forelimb in relation to the hindlimb produced by these relationships in the Ground Standing and Walking primates relative to the condition in the Branch Sitting and Walking primates and the Old World Semi-Brachiators can be explained by a number of mechanical models. Kimura, et. al.(1979) have shown that non-primate terrestrial quadrupeds carry the maprity of their body weight on their forelimbs and efficiently propel their bodies with these limbs, while primates consistently carry the majority of their body weight on their hindlimbs and propel their bodies with these limbs. Stern (1976), based on a theoretical analysis of weight distribution in primates, suggests that the longer the forelimb in primates the greater the amount of body weight carried on the forelimbs. The long forelimbs relative to hindlimbs in the Ground Standing and Walking primates, and to a varying degree in the Part Ground Standing and Walking and Part Branch Sitting and Walking primates in relation to other primates of their body size, therefore, may be an adaptation to more efficient weight carriage and movement in terrestrial locomotion.

In addition, it has been suggested that the advantage of the limb proportions found in the terrestrial primates lay with increased speed and length of stride. Tuttle and Basmajian (1974[a-b]) note that the forelimb acts as a complex second order level system to propel the body weight forward relative to the fixed hand by the function of the retractor muscles of the shoulder, and, at the end of the propulsive phase, by the action of triceps brachii, which extends the elbow. The elongation of the forelimb as a whole results in both increased speed and increased length of stride. In this context, Proust and Susman (1969) have commented on the efficiency of the gait of terrestrial quadrupeds at high speeds for which the relative length of the limbs results in a horizontal placement of the shoulder

and hip above the substrate.

There have also been a number of hypotheses suggested to explain in functional terms the relatively short forelimb in relation to the length of the hindlimb in the Branch Sitting and Walking and the Old World Semi-Brachiating primates. Based on a series of photographs of Papio in horizontal walking and vertical climbing, Jolly (1965) notes a flexed propulsive stage in climbing which is completely lacking in terrestrial progression. During flexed propulsion there is a slight flexion of the shoulder, sharp flexion of the elbow and the pull is exerted along the axis of the limb. The body is drawn inwards and upwards, then the whole limb is retracted. This type of movement emphasises power, and although Jolly notes that Papio is not particularly adapted to arboreal climbing, he also emphasised that a flexed propulsive state is found in more arboreally adapted primates and, in fact, in these forms comprises a larger proportion of the total forelimb propulsion than is observed in Papio. Forelimb adaptions in animals habitually moving in this fashion would be expected to show forelimb adaptions different from those observed in terrestrially adapted primates related to speed and stride length, i.e. power adaptations. And they would be expected to show a shortening of both the humerus and radius, which would infer an increased mechanical advantage to the flexor muscles of the forearm essential in the initial flexing of the elbow effecting an elevation of the centre of gravity. A reduction of the length of both of these bones would also give an increased mechanical advantage to the flexors of the shoulder which, upon retraction, would draw the centre of gravity further upward in relation to the flexed forelimb. In climbing movements the legs also exert a propulsive thrust and the relative participation of both limbs in elevating the animal is yet to be studied in detail. However, the point remains that in a climbing posture the forelimb is used in qualitatively different fashion than it is in terrestrial locomotion. The degree to which this can be considered the determining factor in the development of short forelimbs in the arboreal Cercopithecoidea is largely related to the importance of and type of climbing in their locomotor adaptation, as well as to the importance of the forelimb in lifting the centre of gravity.

Proust and Susman (1969) have offered an alternative locomotor interpretation for the development of short forelimbs relative to hindlimbs in arboreal primates. They suggest that this intermembral relationship may be a specific adaptation to above branch locomotion on inclined surfaces where the relatively short forelimbs allow the animals to approach an inclined surface as if it was level ground. Their hypothesis is based on gait analysis of a subadult squirrel monkey on inclined surfaces of various slopes. The animal performed most efficiently on a slope of 16°, which was the slope which produced an horizontal orientation of the hip and shoulder given the absolutely shorter forelimbs than hindlimbs. They conclude that advancement and retraction of the limbs on such a slope can proceed as if the animal were a cursorial mammal running on level ground.

The degree to which this model can be accepted as a plausible explanation for a low intermembral index in arboreal primates is dependent on the degree to which speed in such circumstances can be considered a selective advantage. The locomotor efficiency in the experiments dropped radically as the substrate slope deviated in both directions from 16°. It is unlikely, given the variety of substrate slopes available to an arboreal primate, that efficiency would be selected for based on a specific degree of substrate incline. This is in addition to the point that such arboreal primates would be expected to descend these inclines at a frequency equal to their ascent. Further information is needed in relation to the entire locomotor repertoire of these primates as well as of primates of different body sizes and arboreal niches which show the same characteristic low intermembral index before this hypothesis can be considered more than an interesting suggestion.

Fleagle (1977) has offered additional hypotheses relevant to the reduced forelimb relative to hindlimb in arboreal monkeys. He explains the significantly lower intermembral index of Presbytis melalophos in relationship to Presbytis obscura by the greater amount of leaping behaviour of Presbytis melaophos in its locomotor

repertoire. In his view this could be achieved by either lengthening of the hindlimbs or shortening of the forelimbs. Lengthening of the hindlimbs in a leaping animal would act to increase the distance over which the accelerating force is exerted and thus either decrease the necessary magnitude of the force or increase the distance of the jump. Reduction of the forelimbs is interpreted as reduction of excess mass that must be accelerated during the leap.

Although these hypotheses suggest various advantages for the equal length of the forelimb and the hindlimbs in terrestrial primates on the one hand, and for short forelimbs in relation to hindlimbs in arboreal species on the other, they all suffer from the lack of comparative locomotor and biomechanical data. However, the work by Kimura, et. al. (1979 and Stern (1976)), which links the length of the forelimb to the position of the centre of gravity to efficiency in terrestrial locomotion, deserves further analysis in a number of contexts. Of particular importance is the relationship between the energetics of primate locomotion, the unique primate gait pattern (Howell, 1944), the possession of a clavicle in primates and primate body proportions, not only in the above branch/level surface feeders, but also in the remaining primates.

IX 9. Below Branch Feeders

The advantage of a low intermembral index in an above branch setting is not shared by those primates who incoporate some degree of suspensory behaviour in their locomotor and feeding repertoire (pongids, hylobatids, and New World Semi-Brachiators). These primates are all characterised by a higher humero-femoral index than are the above branch/level surface feeders (Fig. IX.1). The magnitude of the humero-femoral index, as well as the intermembral index and the brachial index, is dependent on both body size and specific niche exploitation in the below branch setting.

The smaller bodied primates which incorporate below branch activities in their locomotor repertoire are the New World Semi-Brachiators, Alouatta, Lagothrix, Brachyteles and Ateles and the Old World Semi-Brachiators, Hylobates and Symphalangus. Of these,

Alouatta and Lagothrix are not characterised by an unusual elongation of either their forelimbs or their hindlimbs in relation to body weight as are the remaining smaller bodied primates in this below branch category. Both Alouatta and Lagothrix are characterised by intermembral proportions which are equivalent to the Ground Standing and Walking primates and to the Part Ground Standing and Walking primates. However, they differ from these primates in their low brachial index. They are characterised by both a significantly long humerus in relation to their femur lengths and a significantly short radius in relation to their humerus lengths in comparison to these primarily terrestrial primates. The humero-femoral index, intermembral index and brachial index characteristic of Alouatta and Lagothrix show a qualitatively different pattern from the above branch feeding arboreal primates of their general body size (Branch Sitting and Walking primates and Old World Semi-Brachiating primates). Although the arboreal locomotor behaviour of these two general types of primates has not been analysed in detail, the following points can be argued from their proportional differences.

1. The long forelimb characteristic of Alouatta and Lagothrix in relation to the above branch feeders of their general body size would increase their length of grasp. This would be an advantage where it is necessary to reach out and grasp a brach to either secure a hold to support the body or to reach of piece of fruit. In a below branch setting this would be of crucial importance, while in the above branch setting the body weight would be supported by the branch upon which the animal was standing.
2. The low brachial index in these primates would result in a forelimb which favoured power. The lever arm would be short in relation to the power arm and these primates would, therefore, sacrifice speed in forearm movement in favour of power. This situation would be advantageous in forelimb suspended feeding postures, which would favour relatively slow deliberate movements rather than more rapid acrobatic suspended locomotor behaviours.

The remaining smaller bodied primates which incorporate below branch activities in their locomotor repertoire, Hylobates, Symphalangus, Ateles and Brachyteles are characterised by unusually long forelimbs and, to a lesser extent, hindlimbs, for their body weight as well as a high intermembral index and a high brachial index. The forelimb elongation in these species appears to be adapted to their particular type of acrobatic below branch adaptation.

Fleagle (1974) has described in detail the pendulum action of the slow brachiation of the siamang. These primates maximise their forward momentum by flexing or extending the legs and free arm during progression. This alternatingly raises and lowers the centre of gravity and thereby maximises kenetic energy. The principle is the same as a child on a swing who achieves momentum by pumping its legs. This type of locomotion thereby requires very little energy expenditure. In this type of progression the length of the forelimb would be directly proportional to the distance covered per swing and would be advantageous in terms of either speed or energy expenditure per distance covered. Fleagle notes that in instances when siamangs do not employ the pumping mechanism that active rotation of the body around the hand and brachial flexion becomes more important in exerting momentum. Tuttle (1969, 1970) also comments on the significance of brachial flexion in gibbon and siamang progression. Again, in this case a long forelimb and high brachial index would result in maximum speed. Although Tuttle (1975) has questioned the extent to which rapid bimanual suspensory progression is characteristic of Ateles, Jenkins et. al. (1978) have demonstrated that shoulder and elbow movements also contribute to the efficiency of the swing in terms of the dynamics of a pendulum in the locomotion of these New World primates.

IX 10. The Brachial Proportions of the Large Bodied Below Branch Feeders and Homo Sapiens

The large bodied pongids and Homo share many features of the shoulder girdle, vertebral column, forelimb and hand, which attest to a common heritage of below branch behaviour (Cartmill

and Milton, 1976, Stern, 1971, 1976, Tuttle, 1976). This group shows a wide variation in their brachial proportions, however, (Fig. IXl). The relative length of the forearm in relation to the upper arm correlates with the amount of suspensory behaviour in their locomotor repertoire. Pongo, the most arboreal of this group, has the longest radius for its humerus length, followed by Pan, Gorilla and Homo. Tuttle and Basmajian (1974) have recently demonstrated that m. brachialis is the primary felxor of the elbow in both suspensory and manipulatory functions, and have offered further support to Sir Arthur Keith's hypothesis concerning the efficiency of a long forearm in suspensory locomotion (1926). M. brachialis acts in a third order lever system. The greater the length of the forearm distal to the attachment of m. brachialis, the greater is the speed as well as the length of the grasp. Martin (1934) as well as Tuttle and Basmajian (1974) emphasise the reduction of the length of the ulnar olecranon process in this context. Martin (1934) notes that with the exception of Gorilla, which has the shortest olecranon process in the higher primates, the relative reduction of the olecranon correlates with the degree of suspension in the locomotor repertoire. After Gorilla, the smallest olecranon process is found in Hylobates, followed by Pongo, Pan, Homo and the Cercopithecidae. Tuttle and Basmajian (1974) interpret the short olecranon of the gorialla in the context of its knuckle walking locomotion and particularly the advantage of the hyperextension of the elbow. They interpret the advantage of this hyperextension in the context of stabilisation of the elbow joint against torque forces during load bearing and note also that flexion of the elbow joint would interrupt alignment of the upper arm and forearm which is required for effective employment of the forelimb as a propulsive prop.

Therefore, if speed of movement and length of grasp/span are the important features in below branch feeding and locomotion, a long forearm in proportion to the upper arn would enhance these factors. Keith (1926), LeGros Clark (1959) and Tuttle and Basmajian (1974) assume that the ancestral brachial relationships for the Hominoidea was a long forearm in relation to the upper arm. Keith noted that once suspensory movement was reduced in the locomotor

repertoire a long forearm would become disadvantageous. The forelimb in the primates (with the exception of Homo) serves a dual function of locomotion and manipulation. Keith (1926) argues that elongation of the forearm would impair speed and precision of elbow flexion during manipulation and that the most efficient brachial proportions for moving light loads is a relatively long upper arm and a short forearm as found in Homo. Keith was not aware that Gorilla also possessed a short forearm. Tuttle and Basmajian (1974) also interpret the short forearm of Gorilla in the context of manipulatory functions. This is not entirely convincing. In view of the large size of this primate, the olecranon reduction which Tuttle and Basmajian have interpreted in the context of terrestrial locomotion, as well as the modifications of the hand for efficient knucklewalking (Tuttle, 1967), the short forearm might also be explained in locomotor rather than manipulative terms. Gray (1943) has noted that in large heavy muscled terrestrial mammals, where speed in movement is not a factor, the most efficient limb proportions would be short distal segments in vertical alignment with the more proximal segments, In view of the weight of the gorilla, its use of the forelimb as a propulsive prop and the vertical alignment of the bones of this limb, a short forearm would be consistent with Gray's graviportal model.

There are two additional points which are of interest in this context. Firstly, in spite of the relatively short forearm in comparison to the length of the upper arm in Gorilla, the intermembral index is still high. As suggested by Stern (1976) a high intermembral index would result in an anterior placement of the body centre of gravity. Kimura et. al. (1979) have argued that this placement of the centre of gravity is advantageous in terrestrial locomotion. Therefore, in spite of the reduction of the length of the forearm, Gorilla would be well adapted to terrestrial locomotion in terms of placement of the centre of gravity. Secondly, the large-bodied Pleistocene cercopithecine Simopithecus is characterised by not only a short radius for its humerus length, but also a short femur for its humerus length. In its limb proportions it is the closest primate parallel to the extant gorilla and it is

of undoubted terrestrial locomotion (Jolly, 1972). It therefore appears likely that the short forearm in the gorilla in comparison to the remaining large bodied pongids is an adaptation to terrestrial locomotion.

The short forearm in Homo, however, is best explained by the manipulative model. Not only is there no convincing evidence that Homo ever passed through a knuckle walking stage (Tuttle, 1969, Tuttle and Basmajian, 1974b) but the relatively large olecranon in Homo would contribute to power in manipulative functions which would be of significance in tool manufacture as well as in the use of projectile weapons.

The evolution of the variety of brachial proportions in the Hominoidea will be discussed in relation to the available fossil evidence in Section IX.22. Although the concensus of opinion has been that the ancestral brachial pattern was a long radius in relation to the length of the humerus, there has been little discussion of the specific length relationships in an evolutionary context. The implicit assumption in modern literature is that the ancestral pattern was as extreme as seen in Pongo or even in Hylobates (Section II.4). There is no evidence for this in the fossil record. Considering the specific nature of the locomotor adaptations in Pongo and Hylobates it is unlikely that either morphological pattern would provide the ancestral pattern from which the brachial proportions in the modern hominoids evolved.

IX 11. The Intermembral Proportions in the Large Bodied Below Branch Feeders and Homo sapiens.

The large bodied pongids are characterised by the highest intermembral index of any of the higher primates. There are currently two mechanical models for such high intermembral indices in these primates. One of these models relates to requirements of terrestrial locomotion while the other relates to the requirements of a large bodied primate in an arboreal niche. The terrestrial model has been discussed in Section IX.8. A high intermembral index results in an anterior placement of the body

centre of gravity. This appears to be an advantageous situation for terrestrial locomotion (Kimura, et. al. 1979). The arboreal model has been termed the vertical support model (Cartmill, 1974, Jungers, 1977, 1978). According to this model a large bodied primate is efficient in climbing vertical trees only if it has a high intermembral index. The long forelimbs allow the primate to lean away from the tree while the short hindlimbs allow contact of the feet with the tree at a position close to the centre of gravity of the animal. Thus, the resultant force produced by gravity and the body weight of the animal will be directed toward the tree and reduce the possibility of slippage.

Because the extant pongids engage in some degree of vertical climbing in their locomotor patterns, the vertical support model might appear to be the most logical explanation for the proportional relationships in these primates. However, the substrate preferences of the extant primates do not necessarily rule out the terrestrial model. Fossil evidence suggests that during the Middle and Late Miocene periods, pongids (Sivapithecus, Dryopithecus) were widespread in Europe and Asia. Recent paleoecological evidence (Andrews, in press, Tattersal, 1969) suggest that many of these primates were occupying sparsly forested or open country environments. These environments, depending on the degree of forestation, would emphasise varying amounts of terrestriality in these primates. In addition, Smith and Pilbeam (1980) have recently drawn attention to giant Pleistocene orangutans in Asia. They have suggested that by virtue of their size it would be unlikely that they were arboreal in their locomotor habits. In addition, they have also raised the possibility that the modern orangutans of Borneo and Sumatra are dwarfed descendants of these ancestral larger forms. It is interesting to note in this context that Vrba (1979) has drawn attention to features of the scapula in Pan and Gorilla which are connected with the weight supporting function of the forelimb in terrestrial progression.

A high intermembral index appears to be mechanically advantageous in both a terrestrial and arboreal setting. As a result, limb proportions developd in one locomotor niche would be preadaptive in the other. Both models appear to be weight

dependent, however, extant primates exhibiting either locomotor pattern do not provide a continuous weight series which would give an empirical data base to study the effects of increasing weight, intermembral proportions and terrestrial or arboreal locomotion. Fossil specimens do extend the weight ranges of the extant species, however, the post crania of these fossils are generally too fragmentary to provide conclusive information. In addition, theoretical analyses within the framework of either model have not proceeded to the point of predicting the ideal intermembral proportions for primates of different body weights. However, on the basis of the allometric comparison the length of the hindlimb and the length of the forelimb in extant higher primates (Section V 14), gross differences in intermembral proportions cannot be considered to be the result of allometric increase with increasing body weight. In spite of the conclusions of Biegart and Maurer (1972) (Section IX. 2), the intermembral proportions of the extant apes represent a qualitative shift from those of the smaller bodied higher primates. This shift was apparently in response to specific locomotor requirements.

Homo sapiens has the lowest intermembral index of any higher primate. However, Homo sapiens is consistent with the allometric trend characterising the smaller bodied higher primates in the relationship between the length of the femur and the length of the humerus and in the relationship between body weight and the length of the hindlimb. In these proportions Homo sapiens appears to preserve the allometric relationship of the smaller bodied higher primates, and particularly the New World Semi-Brachiators, Alouatta and Lagothrix, to a greater extent than do many of the large bodied extant pongids. The deviation of the Homo sapiens in intermembral relationships from the smaller bodied higher primates results primarily from the reduced length of the radius in relation to the length of the humerus in Homo sapiens. As previously argued, this reduction in radius length can be explained by the freedom of the forelimb from locomotion and its use as a manipulative organ.

Under the assumption that large bodied size in either a quadrupedal terrestrial or arboreal niche results in a high inter-

membral index, the conclusion is unavoidable that the early hominids assumed a bipedal form of locomotion at a body weight below that which would require a short hindlimb in relation to the length of the forelimb. The evolution of bipedal locomotion will be discussed in greater detail in Section IX. 23. The hindlimb of Homo sapiens, which appears to be so long in relation to body weight when the extant pongids are used as a comparative sample, is not at all unusual when the smaller bodied high primates are included in the allometric analysis. The similarityin hindlimb proportions between Homo sapiens and these smaller bodied primates suggests that it is unlikely that Homo sapiens did not have its ancestry in primates of intermembral proportions similar to those of the extant great apes.

IX. 12. The Crural Proportions in the Higher Primates.

When the length of the femur is compared directly with the length of the tibia, there is a highly correlated, consistently negative allometric relationship across the entire sample of higher primates (Sections V.4. & VII.5). This relationship holds true, irrespective of the relative length of the hindlimbs in relation to body weight, i.e. the long hindlimb in relation to body weight in Hylobates and the short hindlimb in relation to body weight in the great apes. Therefore, the longer the length of the femur, the shorter the tibia will be in relation to it.

These results indicate that as the length of the femur increases, the femoro-tibia joint takes up an increasingly distal position on the lower limb. Because both the length of the femur and the length of the tibia have a high correlation with body weight in the Group1 primates, it can be concluded that within this sample as body weight increases the femoro-tibia joint takes up a more distal position of the lower limb. This is in direct agreement with Gray's hypothesis of a greater mechanical advantage in a larger animal of a more distally placed joint (1968).

The consistency in the relationship between the length of the

femur and the length of the tibia has interesting implications for the smallest bodied Old World higher primate, Cercopithecus talapoin. Cercopithecus talapoin has been observed to incorporate a degree of vertical clinging and leaping in its locomotor pattern. Cercopithecus talapoin, as well as the vertical clinging and leaping prosimians, are characterised by relatively long tibias in relation to the length of their femora. It has been suggested that C. talapoin is a dwarfed descendent of a larger bodied cercopithecine. (Rollinson, 1975, in the context of the manipulative ability of its hand and feet, Napier, pers. comm. & Rudder, pers. comm. in the context of its reproductive anatomy). If C. talapoin is a dwarfed version of a larger bodied cercopithecine, and this dwarfing occurred along the negative allometric slope characterising the relationship between the length of the femur and the length of the tibia in the higher PRIMATES, the relatively long tibia for the length of the femur in C. talapoin would result as a by product of this dwarfing rather than as a specific adaptation to vertical clinging and leaping locomotion.

In addition, the highly correlated trend between the length of the femur and the length of the tibia makes possible the prediction of the length of one bone from the length of the other in any anthropoid primate, in spite of the locomotor pattern or of the shortening or lengthening of the hindlimb in relation to body weight. This is potentially highly valuable in the reconstruction of the hindlimb length of fossil primates that are known only from the length of the tibia or of the femur. Reconstructed hindlimb lengths for a number of fossil primates are presented in Section VII.5.

IX 13. Locomotor Adaptations in the Miocene Hominoidea.

There are eight species of ape-like anthropoid primate from the Miocene for which there is well described post cranial material (Table III. 3). All of these species are presently, or at one time have been, considered to be members of the Hominoidea. The post cranial material has generated considerable debate over the locomotor patterns it represents. The debate has centred on the similarity of this material to post crania of the extant greater and lesser apes, and, particularly, on the recognition of features in this material

which would suggest either a brachiating (arm swinging) or knuckle-walking locomotor behaviour. In recent years, however, as the result of accumulating information on primate locomotion in the wild, emphasis has shifted away from brachiation as the common locomotor feature of the hominoids. Slow deliberate climbing during feeding, or below branch forelimb assisted climbing has replaced brachiation as the common locomotor feature (Fleagle, 1976), and parallels in morphology have been drawn between some of the Miocene fossil primate post crania and the extant below branch feeding primates (Morbeck, 1972, 1975, 1976, Schon and Ziemer, 1973). Although body size has been taken into consideration in the analysis of locomotion in extant primates, this has not been concistently the case with the interpretation of the locomotor capabilities in the Miocene primates. In the following discussion the Miocene primates are compared with modern primates, and their locomotor patters, on the basis of body size, with two purposes in view. The first purpose is to distinguish above and below branch feeders in the size range where this dichotomy exists in modern primates. The second purpose is to examine the morphology of the larger bodied forms in both an allometric and functional context.

IX. 14. Body Weights of the Miocene Primates

The interpretation of locomotion in the Miocene primates should involve the distinction between above branch feeding and below branch feeding behaviours, as well as the degree of morphological similarity or difference with the extant anthropoid pr mates of different locomotor types within these broader categories. A first step is to determine the body weight of the fossil primates in order to provide a basis of comparison with the body weight ranges of the locomotor categories in the extant higher primates. Analysis of the allometry of higher primates post cranial bones has shown that there are a number of post cranial parameters which have a constant relationship with body weight across the entire higher primate sample and can be used to give a general indication of body weight for the fossil primates (Chapter VIII). Fig. IX.2 provides the weights of the Miocene primates in comparison

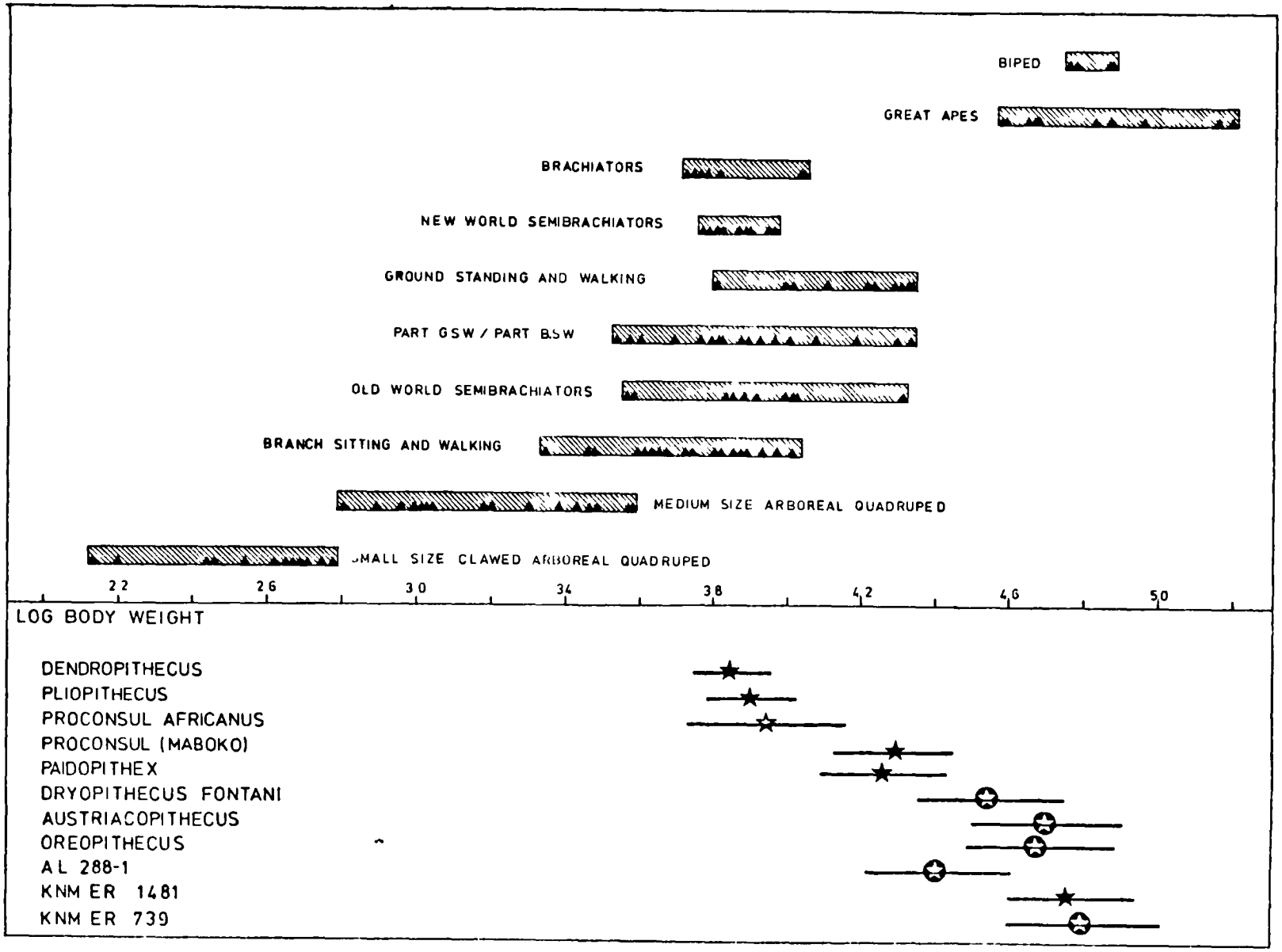

Fig. IX.2. The relationship between body weight and locomotor category for extant and fossil

with the weights of extant higher primates of the different locomotor categories. The Miocene primates fall into three general weight groupings. Dendropithecus macinnesi, Pliopithecus vindobonensis and Proconsul africanus fall within the weight range of approximately 5,000 to 10,000 grams and, therefore, on the basis of weight cannot be excluded from any of the six locomotor groupings characterising the extant primates of this weight range and could equally well be either above or below branch feeders. Proconsul sp. and Paidopithex rehenansis both suggest a weight of approximately 20,000 grams. These primates fall into the upper weight range of the extant Old World monkeys (Ground Standing and Walking, Part Ground Standing and Walking and Part Branch Sitting and Walking, and Old World Semi-Brachiation) and well below the weight range of the extant great apes. The remaining Miocene primates, Dryopithecus fontani, Oreopithecus bambolii and Austriacopithecus weinfurteri, fall into the weight ranges of the extant great apes and human beings.

Based on the weight distributions, the following questions relevant to locomotion in these fossil primates emerge.

1. Is there evidence for an above or below branch feeding adaptation in the size range represented by Dendropithecus Pliopithecus and Proconsul africanus?

2. Do Proconsul sp. and Paidopithex suggest a locomotor adaptation similar to the extant primates of their body weights?

3. What is the similarity of the large bodied Miocene primates to the extant great apes?

4. What can be deduced in relation to the evolution of bipedal locomotion?

IX 15 Evidence for an Above or Below Branch Adaptation in the Small Bodied Miocene Hominoidea

Three of the Miocene primates fall into the weight range between 5,000 and 10,000 grams, Pliopithecus vindobonensis, Dendropithecus macinnesi and Proconsul africanus. For two

of these primates, Pliopithecus vindobonensis and Dendropithecus macinnesi, there is sufficient post cranial evidence to include them in the analysis of the intermembral index, humero-femoral index and brachial index which distinguishes between extant above branch/ level surface feeders and below branch feeders (Fig. IX. 1).

Pliopithecus, for which there is good post cranial material that allows the accurate reconstruction of limb indices (Zapfe, 1960), clearly falls within the above branch feeding pattern. It is most similar in its proportions to the Ground Standing and Walking primates and to some of the Part Ground Standing and Walking and Part Branch Sitting and Walking group (Fig. VII.5 and Fig. VII. 6). This suggests that Pliopithecus was primarily an above branch form. This interpretation is consistent with a number of recent multivariate morphometric analyses of the forelimb joints of Pliopithecus that emphasise the phenetic similarity of this primate with the Cercopithecidae. Ciochon and Corruccini (1977) suggest that the shoulder joint of Pliopithecus has its closest affinity with (in increasing order of distance) Presbytis, Cebus, Nasalis, Macaca, Aotus. Morbeck (1979) suggests that the elbow joint is Presbytis-like and Corruccini, Ciochon and McHenry (1975) suggest that the wrist joint was phenetically most similar to Papio. In addition, these authors, as well as Andrews and Simons (1978) have pointed out a number of qualitative features of the forelimb of both Pliopithecus and Dendropithecus which show cercopithecid phenetic affinities. These features appear to be designed to limit mobility of the forelimb in favour of stabilisation and would be consistent with an above branch feeding adaptation. This interpretation is also consistent with the original interpretation of the locomotor capabilities of Pliopithecus (Zapfe, 1960). Zapfe suggested, both on the basis of the intermembral proportions and ecology, that Pliopithecus would have been most similar to the extant Papio and Macaca in its locomotor capabilities even though the general morphology of the post crania does not agree with either that of Papio or Macaca.

The second species, Dendropithecus macinnesi, is more

difficult to include in this analysis. The limb bones of this form are incomplete and their lengths were originally reconstructed using Ateles and Hylobates as models (LeGros Clark and Thomas, 1951). As a result, the lengths of these bones may be overestimated. However, even if the bones of the forelimb of Dendropithecus are reconstructed to be considerably shorter than suggested by LeGros Clark and Thomas (1951), the fossil still falls well within the range of variation in the above branch category (Fig. IX.1)
Many of the significant joint surfaces are missing in this fossil and it is, therefore, difficult to support or reject an above branch adaptation for this primate on morphological criteria. However, because of the clear distinction between above branch feeders and below branch feeders on proportional criteria, it is highly likely that Dendropithecus engaged in above branch feeding.

It has frequently been argued in the literature that Pliopithecus and Dendropithecus are ancestral to Hylobates (LeGros Clark and Leakey, 1951, LeGros Clark and Thomas, 1951, Simons and Fleagle, 1973, Fleagle, 1975). Recently Andrews and Simons (1978) argued that Dendropithecus is further advanced in the direction of modern hylobatids than is Pliopithecus. It is true that the fauna associated with Dendropithecus material indicates an arboreal adaptation for this primate. However, this could be associated with either an above branch or a below branch feeding adaption. Andrews and Simons base their conclusions primarily on the gracile limb bones of Dendropithecus. They interpret the gracility of the limb bones as an indication of suspensory locomotion, while claiming that Pliopithecus had much more robust bones. Section VII.4. has shown that this interpretation is not correct. Pliopithecus, Dendropithecus and Proconsul africanus all show a humerus of similar gracile proportions, while Dendropithecus has a more robust femur than does Pliopithecus, and would be similar in proportions to the femur of the larger bodied Miocene primate Proconsul sp. Maboko and Paidopithex rehenanus. There is, therefore, no reason on the basis of the gracility of the skeleton or on the basis of limb or bone lengths to suggest that Dendropithecus is more closely related to Hylobates than is Pliopithecus.

Remane (1965), Delson (in Delson and Andrews, 1975), Groves (1972), von Konigswald (1968, 1969) and Ciochon and Corruccini (1977) emphasise the primitive morphology of these primates and imply that Pliopithecus and Dendropithecus should be considered to be conservative early catarrhines. Groves (1972) agrees with Remane (1965) and suggests that Pliopithecus be included in the family Pliopithecidae along with Aegyptopithecus, Propliopithecus and perhaps Oligopithecus. He essentially views Pliopithecus as a Miocene survivor of this Oligocene group. Corruccini and Ciochon (1977) emphasise that this family would, therefore, contain Dendropithecus as well as the common ancestors of both the Cercopithecoidea and Hominoidea. The brachial proportions of Pliopithecus as well as details of its limb morphology (Corruccini and Ciochon, 1977) might indicate a complex of shared derived features with the Cercopithecoidea, however, the aberrant ear region of Pliopithecus (Zapfe, 1960) argues against this hypothesis and the question is best left open for the present.

The third small bodied Miocene primate is Proconsul africanus. This fossil is represented by a forelimb skeleton. Because it lacks an associated hindlimb, it is impossible to include it in the analysis of the intermembral index or the humero-femoral index. However, body weight can be predicted for this fossil from the length or the circumference of its humerus (Chapter VIII). In the comparison between brachial index and body weight Proconsul africanus closely resembles the New World Semi-Brachiating primates and has no parallel among the Old World primates which engage in above branch activities in its body size range (Fig. IX.3). This suggests that there were primates in the Old World during the Miocene, which no longer exist in their generalised form in the Old World, that engaged in a below branch feeding adaptation.

This interpretation is similar to the original interpretation for the locomotion of Proconsul africanus suggested by Napier and Davies (1959). They concluded that the morphology of the forelimb and available hand bones of Proconsul africanus represented a mosaic of primitive arboreal quadrupedal features and specialised

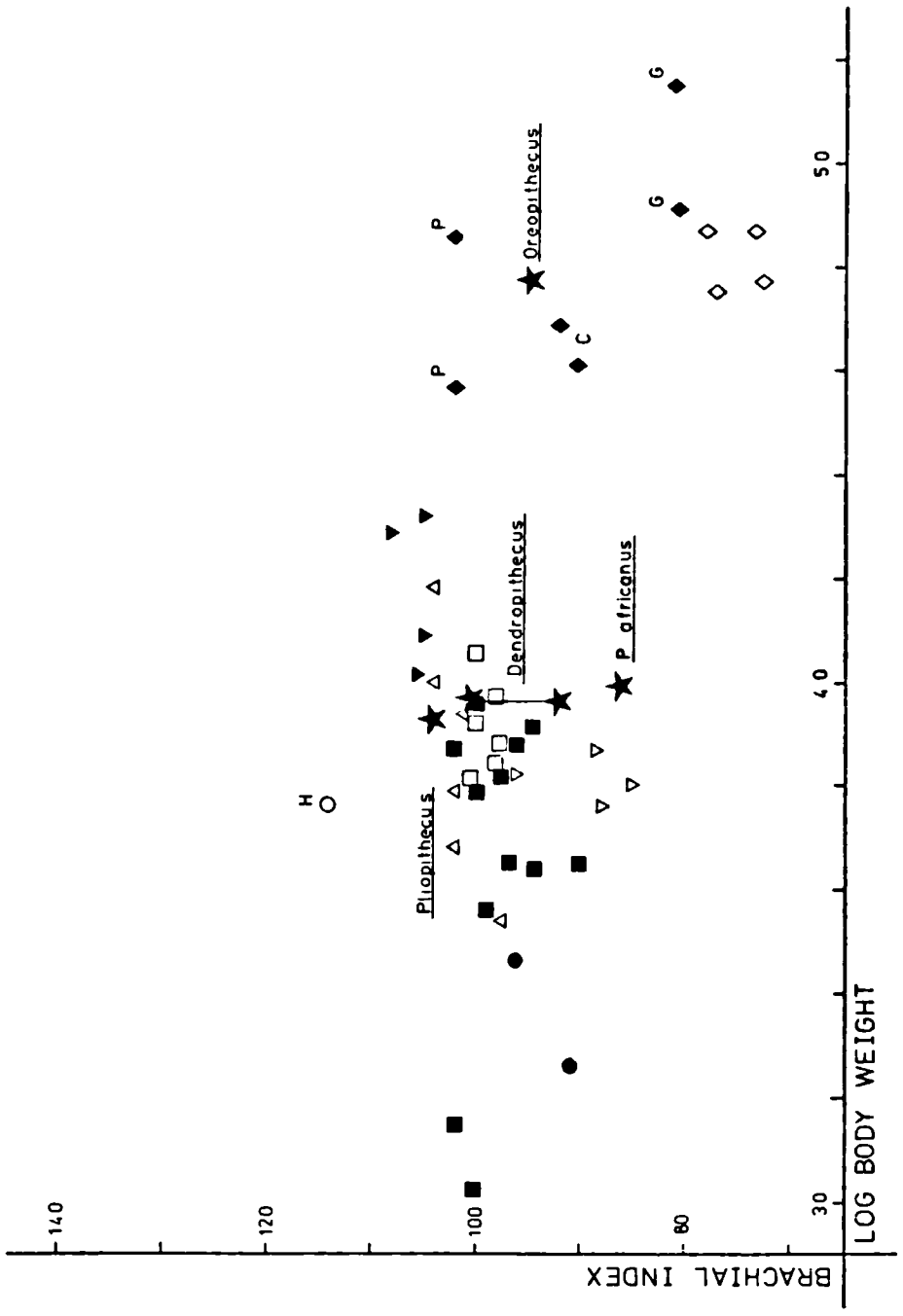

Fig. IX.3. The relationship between body weight and the brachial index including selected fossil higher primates.

brachiating features. They definitely concluded, however, that there was no evidence in the morphology of the forelimb of a terrstrial quadrupedal adaptation. In their view, Proconsul africanus represented a level of generalised brachiation (or semibrachiation) similar to the modern genera Presbytis and Ateles. Modern analysis of primate locomotor behaviour in the wild and of the relationship between morphology and locomotor behaviour has shown that semibrachiation is not a uniform locomotor category and that the arm suspension behaviour (semibrachiation) of the New World primates differs considerably from the semibrachiation of the Old World primates in which arm suspension is a rare and infrequent occurrence (Rose, 1973). Although this work has emphasised the inadvisability of lumping the New and Old World Semi-Brachiators in a single locomotor category for comparative purposes it has not seriously altered Napier and Davis' (1959) interpretation of the locomotor behaviour of Proconsul africanus.

There has been recent analyses, however, which have inferred a greater amount of arm suspension in the locomotor repertoire of Proconsul africanus. The wrist joint has been particularly controversial in this context. Lewis, in a series of papers (1965 - 1972) has concluded that the wrist of Proconsul africanus was particularly well adapted for suspensory locomotion. He based this conclusion on his interpretation that the wrist of Proconsul africanus contained a meniscus between the distal ulna and proximal triquetral and that Proconsul africanus possessed certain modifications of the carpal bones in common with the extant Hominoidea. Conroy and Fleagle (1972) accepted Lewis' interpretation of a meniscus containing wrist joint in Proconsul africanus, but rather than interpret it as an indication of suspensory locomotion they interpreted it as indicative of a knuckle walking adaptation arguing that it allowed maximum flexibility at the wrist joint without necessarily reducing the ability of the joint to withstand compressive forces during quadrupedal locomotion. Morbeck (1974), O'Conner (1975), Corruccini et. al (1975) and Schone and Ziemer (1973) have criticised these interpretations on two grounds. Firstly, they have criticised Lewis' use of casts to study the morphology of the wrist

area. The casts at Lewis' disposal were not detailed enough to show the essential facets on the joint surface of the ulna styloid process, which indicate a direct articulation between the styloid and the pisiform and triquetral. The casts of the hamate and capitate were also distorted to a degree to cause serious misinterpretation of the morphology of these bones (Corruccini et. al. 1975, Schöne and Ziemer, 1973, Morbeck, 1975). Secondly, the features used by Lewis to distinguish a brachiating versus a quadrupedal wrist adaptation have been shown to be poor discriminators of these locomotor types (O'Conner, 1975). These authors have built up a convincing argument that the wrist morphology of Proconsul africanus shows no suggestion of the beginning of the major changes which mark the hominoid adaptative radiation. Schone and Ziemer (1973) and Morbeck (1975) suggest on the basis of their analyses of the articular surfaces of the wrist bones that Proconsul africanus is most consistent with the palmigrade quadrupedal stance and locomotor pattern of Alouatta and Ateles, while Corruccini et. al. (1975) on the basis of the multivariate morphometric analysis suggest that the wrist of Proconsul africanus is most similar to Ateles, Cercopithecus and Nasalis.

Zwell and Conroy (1973) have provided an additional line of argument designed to suggest pongid and not monkey affinities for Proconsul africanus. Based on a multivariate analysis of indices presented in Napier and Davis (1959), Proconsul africanus assorts with apes on both the first component which separates quadrupedal Cercopithecidae from both knuckle walkers (Pan and Gorilla) and the quadrupedal arm-swinger (Ateles) and on the second component which separates knuckle walkers from all knuckle walking quadrupeds. They, therefore, concluded that the total morphological pattern of the forelimb is pongid-like and not monkey-like. Corruccini et.al (1975) question their statistical procedures while Morbeck (1975) criticizes their sample size and also points out that the indices used only reflect the distances between various joint centres and related soft tissue, but do not significantly demonstrate the direction and range of movement permitted within the joint complexes. On this basis she disagrees with their conclusions that Proconsul is more

similar to the Pongidae than to the monkeys, was unlike 'semi-brachiating' quadrupeds and was in some way preadapted to a knucklewalking form of locomotion. The present analysis has shown that Proconsul africanus is most similar to Alouatta in its forelimb proportions and to Alouatta, and to a lesser extent, Colobus and Presbytis, in its humerus robusticity and suggests, as does Morbeck, that there is no reason to assume a greater similarity with extant pongids than with these extant species.

The majority of authors who have dealt with the wrist joint have ignored the morphology of the metacarpals and the phalanges. Napier and Davies (1959) concluded that those features of the hand which were most adaptive to a suspensory locomotion (brachiation) were limited to the metacarpals and phalanges. In particular, the hand showed a condition of relatively long metacarpals and phalanges in relation to the total length of the hand. This is in contrast to the primitive pattern of short metacarpals and short phalanges, the generalised hand of the arboreal primates with short metacarpals and long phalanges (Nothoarctus, Cebupithecia, Tarsier, lemuroids, New World primates and thoroughly arboreal Old World monkeys) and the terrestrial hand with long metacarpals and short phalanges. These proportions would be in general agreement with a climbing adaptation, emphasising an efficient grasp and would be expected to increase in importance as body size of the primate increased.

Stern (1976) and Fleagle (1976) have recently suggested that an adaptation to climbing may be the basic locomotor adaptation of the hominoid radiation. It is conceivable that the elongation of the metacarpals and phalanges was the first step in increasing the efficiency of the hand in climbing and as body size and climbing efficiency increased this initial modification was followed by both wrist modification and further modifications of the metacarpals and phalanges. Among the metacarpal and phalangal modifications would be increased ray lengthening, longitudinal curvatures as a response to increased bending moments imposed by lengthening of the fingers, developed flexor ridges on the phalanges and an

emphasis on the ulnar side of the hand (Susman, 1979, Susman and Stern 1979). The morphology of the elbow joint (Napier and Davis, 1959, Morbeck, 1976) would be consistent with climbing adaptation. The movement capabilities have been interpreted as similar to living hominoids permitting full extension and a wider range of pronation and supination than found in extant monkeys. The low deltoid insertion on the humerus would also be consistent with arm elevation in a reaching and climbing locomotor pattern. The reconstructed posterior orientation of the head of the humerus would be a primitive feature in relation to the more medial orientation of the head in the extant hominoidea, however, and as the wrist would be an indication of an incipient climbing/suspensory adaptation.

Napier and Davis (1959) concluded that the brachiating (arm suspension) characteristic of Proconsul africanus could not be regarded as evidence of a new adaptive trend appearing suddenly for the first time in the Lower Miocene of East Africa, but as the inevitable outcome of a long uninterrupted arboreal lineage. This analysis supports this view It is suggested that as body size increased in the lineage, which was unencumbered by the stabilising adaptations of a terrestrial heritage, climbing became an essential selective pressure, producing a change in the morphology of the forelimb in Proconsul africanus and to a greater extent the living Pongidae and that this morphology is only secondarily adaptive to a brachiating or arm suspension locomotor style

Therefore, evidence from the analysis of limb proportions in Pliopithecus vindobonensis, Dendropithecus macinnesi and Proconsul africanus suggests that only Proconsul africanus engaged in below branch feeding activities. In view of the likely below branch feeding locomotor ancestry of the extant hominoids, Proconsul africanus can be viewed as a generalised below branch feeder of a locomotor form which would provide a more likely ancestral type for at least the extant great apes and Homo than any other Miocene fossils for which there is post cranial evidence.

IX 16. The Locomotor Adaptations of the Medium Sized Miocene Hominoidea

The medium sized Miocene primates, Proconsul sp. and Paidopithex rehenanus fall into the upper size range of the extant Old World Semi-Brachiators, the Part Ground Standing and Walking and Part Branch Sitting and Walking primates and the Ground Standing and Walking primates (Fig. IX. 2). It is unlikely, however, that these fossil primates were similar in their locomotor adaptation to the extant primates of their body size range. Paidopithex is represented only by a complete femur (Pohlig, 1865) and Proconsul sp. by a femur and humerus which most likely do not come from the same individual (Chapter III). Therefore, the limb proportions of these primates are unknown. However, the morphology of the femora is different from that of the extant primates of their body size ranges. This is particularly apparent in the confirmation of the proximal end of the femur. In both of these primates the head of the femur projects well over the greater trochanter, while in the majority of the above branch and terrestrial primates the reverse is true. Zapfe (1960) has noted that this is also true of the majority of the fleet footed ungulates and that this feature in the Old World monkeys may be related to rapid quadrupedal running. There are also other differences between these Miocene fossil femora and those of the Old World monkeys. Greatest similarily is found between these fossil femora and those of the below branch feeders, both the New World Semi-Brachiators and the Brachiating hylobatids. This is evident not only in the position of the head in relation to the greater trochanter but also in the straight shaft, the form of the trochanteric fossa, the angle between the neck of the femur and the shaft and in the distal part of the femur in the popliteal region and in the condyles. In addition, there are considerable differences in morphology which separate these femora from those of the extant great apes. The most marked differences are those which relate to the reduction of the length of the femora in the great apes in relation to their body weights. Fig. IX. 4 illustrates the length of the femur in comparison to the transverse diameter of the femur, which is a constant measure

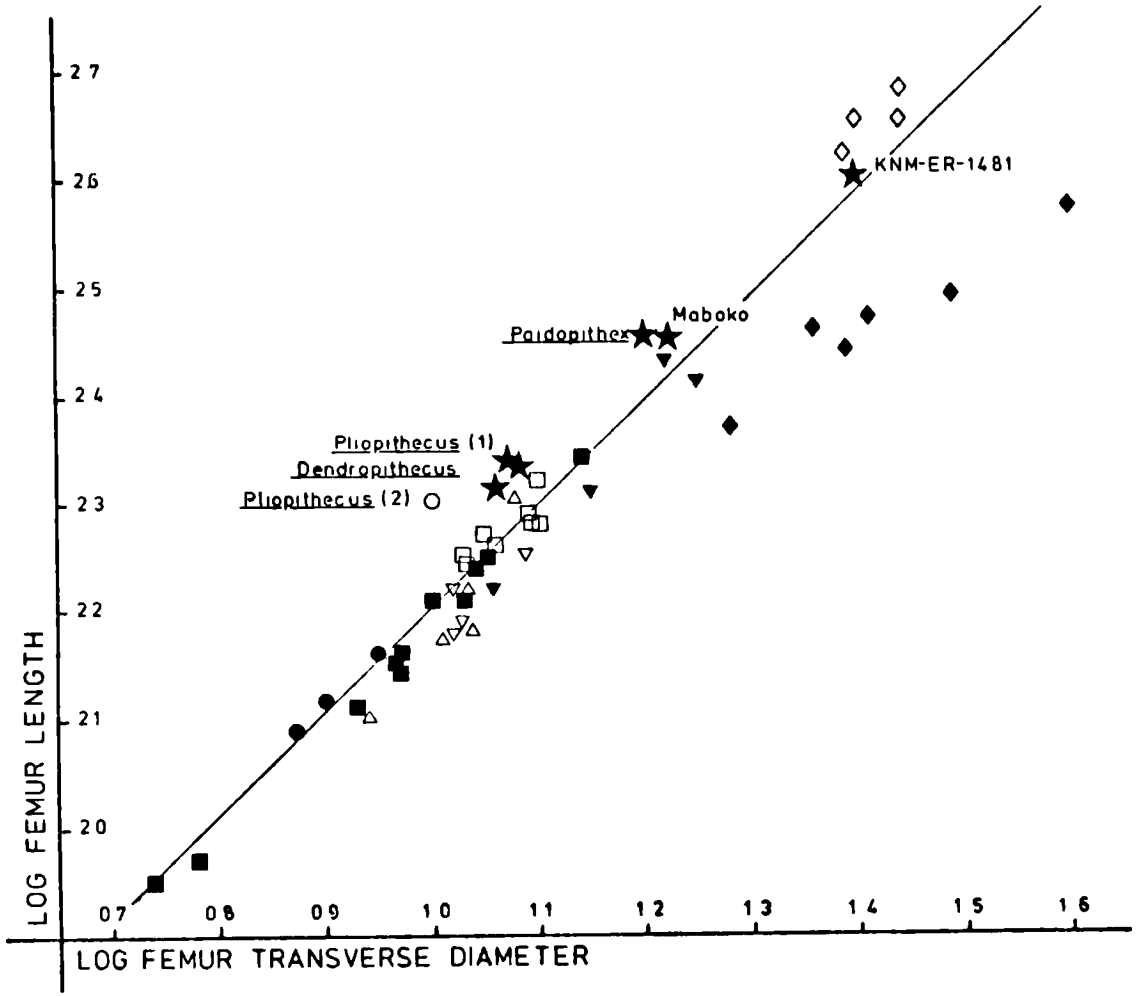

Fig. IX.4. The relationship between the transverse diameter of the femur and the length of the femur including selected fossil higher primates.

of body weight across the higher primates (Chapter VIII). The entire sample, except for the great apes, falls along an isometric principal axis. The great apes deviate from this trend in the direction of a reduced femur for their femur transverse diameters and for their body weights. None of the Miocene fossil primates show a similar reduction.

From this evidence it can be concluded that these Miocene fossil femora do not show the morphology seen in extant above branch feeders or in the extant great apes. However, the similarity in the morphology of these femora and those of the New World Semi-Brachiating primates of a smaller body size suggest that these may represent the generalised morphology of a primate, who either employed a degree of below branch feeding in its behavioural pattern or descended from a primate which was characterised by this behaviour.

Because the Miocene primates, Proconsul sp. and Paidopithex rehenanus are not characterised by a reduced hindlimb, it is probable that they would have been even better preadapted to bipedal locomotion than are the extant great apes. They would have been characterised not only by a longer stride length in relation to their body sizes, but also, more than likely, by a more caudal placement of the total body centre of gravity than are the extant great apes. Theoretical work by Kimura et. al (1978) has shown that efficiency in bipedal locomotion is involved with the development of a heel and postural changes producing an extended hip and knee joints. In their analyses length of the hindlimb does not significantly contribute to efficiency of muscle and joint usage in bipedal locomotion. Based on this work, it is unlikely that selection would favour an increase in the length of the hindlimb, if the ancestral form already was characterised by a short hindlimb for its body size. In this context the Pliocene hominid skeleton, AL-288-1 from Hadar, Ethiopia, is of only a slightly larger body size than that inferred for Pronconsul sp. and Paidopithex (Fig. IX. 2). On morphological criteria this hominid was already an efficient biped (Johanson and White, 1979). In comparison between the length of the humerus and the length of the femur, the only two bones for which length measurements are

available, this skeleton is similar to the New World Semi-Brachiators in its proportions expressed at a larger body size (Fig. VII.5). The femora of Proconsul and Paidopithex would represent a likely hominoid type which could have given rise to the bipedal morphology expressed in AL-288-1 and similar post cranial fragments

Experimental work done by Taylor and Rowntree (1972) on the energetics of primate locomotion has shown that there is no difference in efficiency between bipedal and quadrupedal locomotion in Cebus, Ateles and Pan. There is no reason to doubt that this would also be the case for the prehominids of the Miocene. Wrangham (ms.) has recently suggested that locomotion during feeding may have provided the adaptive situation which emphasised bipedal postures in these primates.' However, whatever the pressure, it is likely that the Miocene hominoids represented by Proconsul sp. and Paido ithe would have been better preadapted to bipedal locomotion than are any of the extant primates of comparable or larger body sizes. The above branch feeding primates would lack the necessary morphological preadaptations resulting from a below branch feeding adaptation, while the extant great apes would be characterised by the disadvantageous short legs for their body weights.

IX. 17. The Locomotor Adaptations of the Large Size Miocene Hominoide

The remaining Miocene primates, Dryopithecus fontani, Oreopithecus bambolii and Austriacopithecus weinfurteri fall within the weight range of the extant great apes and human beings (Fig. IX.2). They are also equivalent in body weight to the estimated weights for the Plio-Pleisticene hominids represented by the KNM-ER-1481 femur (Homo, Leakey, 1973) and the KNM-ER-739 humerus (Australopithecus, Leakey, 1971).

Among the Miocene primates of this body size range Oreopithecus bambolii is represented by a virtually complete skeleton while Austriacopithecus weinfurteri is represented by a humerus shaft and ulna and Dryopithecus fontani by a humerus shaft in the post cranial skeleton. The Austriacopithecus humerus and ulna most likely do not come from the same individual (Chapter III) and, therefore,

only Oreopithecus can be included in the proportional analyses discussed here. In its general proportional pattern as represented in the comparison between brachial index and humero-femoral index (Fig. IX.1) Oreopithecus is unlike any of the smaller bodied above branch feeding primates. It falls generally within the range of the extant pongids, although it is not identical to any of the pongids in its proportions. Its brachial index falls between that of Pan and Gorilla and that of Pongo, while its humero-femoral index falls between that of Pan and that of Gorilla and Pongo. In predicted body weight, Oreopithecus is most similar to Pan troglodytes (male) and falls between the observed mean body weights of the male and female Pongo pygmaeus (Chapter VIII). However, the 95% confidence limits for this predicted weight overlap the weights of the male and femal Pan paniscus, Pan troglodytes and Pongo pygmaeus. The position of Oreopithecus between Pan troglodytes and Pongo in body proportions (Fig. IX.1) suggests that it is more arboreally adapted than is Pan but without the extreme specialisation of Pongo. This interpretation is in agreement with that of Schultz (1960) who viewed Oreopithecus as a slow moving arboreal primate on the basis of its broad chest, shortened lumbar region and robust femur. Although Schultz's conclusion that Oreopithecus is most similar to Gorilla in its body proportions is not supported by these analyses. The extremely low brachial index in Gorilla markedly differentiates it from Oreopithecus.

The skeleton of Oreopithecus is yet to be completely described, however, Zapfe (1960) emphasises the morphological similarities between the ulna of Oreopithecus and that of Austriacopithecus (in the angled form of the proximal shaft, the attachment for the triceps brachii muscles and features of the ulnar tuberosity). However, Zapfe also points out that the ulna of Oreopithecus is much more like that of the extant great apes and human beings than is that of Austriacopithecus. This is evident in the configuration of the trochlear notch, and of the coronoid process and in the reduction of the olecranon. It is in these features that the ulna of Austriacopithe most closely resembles those of the Part Branch Sitting and Walking and Part Ground Standing and Walking primates and the Ground

Standing and Walking primates. However, whether these features indicate a more terrestrial locomotor behaviour in Austriacopithecus than in Oreopithecus or are merely retentions of primitive ulnar morphology in either one of these primates is yet to be determined.

The humerus of Austriacopithecus is similar to Pan in size, the shape of the cross seection of the proximal end, the development of the supinator crest and the configuration of the proximal part of the olecranon fossa. However, it is markedly different from Pan in the forward convexity of the shaft and in the position of the supratrochlear foramen in the radial fossa rather than in the coronoid fossa. In these features it resembles the non-hominoid primates, and in the degree of forward convexity it most closely resembles the plattyrhines (Zapfe, 1960). It is also similar in these features to the smaller bodied Miocene primate Proconsul africanus. However, it differs markedly from the humerus of Dryopithecus fontani which is characterised by a backwards directed convexity of the shaft. This is typical of the humerii of the extant great apes.

The locomotor interpretation of this material is difficult because of the fragmentary nature of the fossils, both in terms of the percentage of the skeleton which is preserved, as well as the completeness of the individual bones preserved. However, there is a marked difference in the morphology of the ulna of Oreopithecus and Austriacopithecus at approximately the same body weight on the one hand and of the humerii of Austriacopithecus and Dryopithecus fontani on the other. On present evidence Oreopithecus and Dryopithecus fontani most closely resemble the morphology of the extant apes of the same body weight range, and particularly Pan, while Austriacopithecus shows resemblances with Pan as well as with the smaller bodied plattyrhine monkeys, the Ground Standing and Walking primates and Proconsul africanus. This suggests a diversity in locomotor type among these similarly sized Miocene primates, but on present evidence a more detailed interpretation of the locomotor types represented by this material is not possible.

IX. 18. The Antiquity of the Below Branch Adaptation

The analysis of the locomotor capabilities of the Miocene hominoids has shown that Proconsul africanus from the early Miocene of Kenya has a postcranial morphology consistent with a below branch feeding adaptation. Although there is no direct evidence of limb proportions in the Oligocene Fayum primates, recent morphological analysis of postcrania assigned to the taxon Aegyptopithecus zeuxis suggests that the pattern of a short radius in relation to the length of the humerus is also characteristic of this taxon. Both metric (Conroy, 1976, Fleagle, 1975) and morphological (Schon-Ybarra and Conroy, 1978) analyses of a proximal ulna fragment from Yale Quarry M (found 1966-1967, assigned to A. zeuxis by Conroy (1974) on the basis of size) show a close similarity with the ulna of Alouatta. Schon-Ybarra and Conroy conclude that the ulna of both A. zeuxis and Alouatta sustained the same compressive, tensile and shearing stresses. In addition, Fleagle and Simons (1978) conclude that the humerus of Aegyptopithecu (distal fragments DPC-1026 and CGM-40123, found in 1977 in the Upper Foesil Wood zone and assigned to A. zuexis on the basis of size) shares a primitive mosaic of features with the Miocene apes and the New World semibrachiators. They conclude that Alouatta provides the best extant model for the forelimb morphology found in A. zeuxis. In addition, two fragments of distal humerii (DPC-1033, DPC-1045) from a smaller bodied Fayum primate (Aeolopithecus or a new undescribed species of Pliopithecus) show close morphological similarity to Aegyptopithecus zeuxis and Alouatta. The similarity of A. zeuxis, Proconsul africanus and Alouatta is also supported by the morphology of the hallical tarsometatarsal joint (Conroy, 1978).

Although these analyses do not prove that Aegyptopithecus zeuxis was characterised by a below branch feeding adaptation, they strongly suggest that this was the case. If it is so, below branch feeding extends back to the very beginning of higher primate evolution.

IX. 19. The Antiquity of the Above Branch Feeding Adaptation

The above branch feeding adaptation has been recognised in the Early Miocene primate Dendropithecus macinnesi and in the Middle Miocene primate Pliopithecus vindobonensis. There is no post cranial evidence from fossils earlier than these Miocene primates which is complete enough to reconstruct limb proportions and include in the allometric analyses discussed here. However, if both Pliopithecus and Dendropithecus are included in the family Pliopithecidae along with Aegyptopithecus, Propliopithecus and Oligopithecus (Remane 1965, Groves, 1972, Corruccini and Ciochon, 1977), this Oligocene and Miocene family would include primates characterised by both major locomotor adaptations (Aegyptopithecus, below branch feeding, Pliopithecus and Dendropithecus, above branch feeding).

Of the extant higher primate families, the Cercopithecoidea the Hominoidea and the Ceboidea, only the Ceboidea include genera with limb proportions characteristic of both major locomotor patterns. Alouatta and Lagothrix are characterised by limb proportions which indicate a below branch feeding adaption while Cebus is characterised by the relatively low intermembral index and high brachial index indicative of the above branch feeders. The point which separates the proportional relationships in the Ceboidea from those in the Pliopithecidea is the body size of the primates. Cebus is of a considerably smaller body size than is either Alouatta or Lagothrix, while Aegyptopithecus, Pliopithecus and Dendropithecus are closer in their predicted body weights. Rose (1973) includes Cebus in the locomotor category of Medium Sized Arboreal Quadrupeds. The primates included in this category range from 603 grams to 3820 grams. Rose interprets these primates to be below the size range which would require specialised locomotor features in order to maintain an arboreal adaptation. However, neither the locomotor behaviour nor the skeletal and soft tissue anatomy of these primates has been studied in detail. From this locomotor category, only Cebus has been analysed in terms of its limb proportions. However, data from Schultz suggests that at least some of the other genera

included in this category (Saimiri, Pithecia) are characterised by limb proportions resembling those of the below branch feeders. The dicotomy of limb proportions within these smaller bodied primates merits detailed study in relation to the specific locomotor patterns characteristic of these primates and in relation to the morphology of the joint surfaces. Until the results of such an analysis are available, it will not be possible to determine the specific adaptive circumstances under which the above branch feeding pattern and the below branch feeding pattern developed in the larger bodied primates.

The extant Cercopithecidae are universally characterised by the above branch level surface feeding adaptation. The earliest fossil evidence of the limb proportions of this group comes from Mesopithecus pentelici. Mesopithecus is a colobine from the Late-Vallesian-Early Turolian to Late Turolian of South and Central Europe. On the basis of its humero-femoral allometric relationships, it falls clearly within the trend for the above branch feeding primates. It is characterised by the relatively short humerus in relation to the length of the femur found in the Branch Sitting and Walking primates, and in the Old World Semibrachiating primates.

There is earlier fragmentary postcranial evidence for the Cercopithecidae from the West Kenya primate sites of Maboko and perhaps Rusinga and Ombo (Early to Middle Miocene). Von Konigswald (1969) placed this material in two species of the genus Victoriapithecus. However, Delson (1975) primarily on the basis of dental evidence, suggests that these species represent the divergence of the twocercopithecid subfamilies, the Colobini and the Cercopithecini. From the small and very fragmentary collection of postcrania, he suggests that these early cercopithecine show evidence of a terrestrial or semiterrest ial locomotion, while the early colobines show features of a fully arboreal lifestyle. If his interpretation is correct the limb proportions characteristic of both the arboreal and terrestrial Cercopithecidae may have been present at this time.

The earliest generally accepted representative of the

Cercopithecidae is Prohylobates tandyi from the Wadi Moghara fauna of Egypt (Early Miocene). However, because this fossil is known only from three fragmentary mandibles, there is no information on its postcranial adaptations. Although on dental criteria these fossils provide the first clear evidence for the evolution of the Cercopithecidae, an Oligocene divergence for this group has also been suggested. Simons (1972) and Kay (1977) consider Parapithecus from Quarry G and from the Upper fossil Wood deposits of the Faynm in Egypt to represent the first appearance of this family. However, postcranial evidence of this primate is not available, and it is, therefore, not possible to assess its postcranial adaptations.

IX. 20. The Evolution of the Above Branch Locomotor Pattern

The previous discussion has shown that the above branch locomotor pattern was present in the Early Miocene genus Dendropithecus and in the Middle Miocene genera Pliopithecus and Mesopithecus. These primates are charcterised by a radius of approximately equal length to the humerus, producing brachial proportions which are consistent with the extant above branch feeders. However, there are two different intermembral patterns represented in these primates. Both Dendropithecus and Pliopithecus are charcterised by forelimbs and hindlimbs of subequal length, a pattern found not only in the extant Ground Standing and Walking primates and the Part Ground Standing and Walking and Part Branch Sitting and Walking primates, but also found in the Asian colobines, Nasalis and Pygathrix. Mesopithecus is characterised by a forelimb of considerably shorter length than its hindlimb and is consistent in this relationship with the extant Branch Sitting and Walking primates. The previous discussion has not approached the question of which intermembral pattern is primitive for the above branch feeding primates. It is necessary to establish this question in order to approach the problem of the adaptive conditions under which above branch feeding developed.

The establishment of the primitive intermembral pattern can be approached through the application of cladistic methodology.

Cladistics was first proposed by Hennig (1966) in order to establish the hierarchial pattern of morphological affinity among animals. There are two fundamental principles of cladistics. Firstly, phylogenetic affinity is proportional to morphological affinity, and secondly, morphological affinity is dependent on synapomorphic (shared derived)characteristics. Synapomorphic characteristics are characteristics which evolved during the period of common ancestry of a particular group of animals subsequent to the divergence of this lineage from a given ancestral point. Synapomorphic characteristics are contrasted to synplesiomorphic characteristics. Synplesiomorphic characteristics are characteristics which are found in the descendent species by virtue of their appearance at the ancestral reference point. Because these characteristics occur at an ancestral reference point they cannot be used to establish affinity between a particular subgroup of the descendent species. Fig. IX.5 illustrates the distinction between synapomorphic characteristics and symplesiomorphic characteristics. In this Figure the ancestral reference point is 'E'. The morphological characteristics of this ancestor (the morphotype) are represented by blank squares. In the descendent species 'A', 'B' and 'C' the blank squares represent synplesiomorphic characteristics. Species 'A', 'B' and 'C' have these characteristics by virtue of their appearance in the ancestral species 'E'. No matter how many of these characteristics species 'B' and 'C' possess in common, they cannot be used to establish a closer affinity between 'B' and 'C' than either of these species has with species 'A'. The presence or absence of these characteristics in species 'A', 'B' or 'C' reflect only the adaptive circumstances of these species during their development from the ancestral morphotype. It is only those characteristics shared by 'B' and 'C' which developed subsequent to their divergence from 'A' (the synapomorphic characteristics) which can be used to establish a more recent common ancestry between these species than between either of these species and species 'A'. In Fig. IX.5 these characteristics are indicated by 'X'. The characteristics in Fig. IX.5 indicated by a wavy line in species 'B' and a diagonal line in

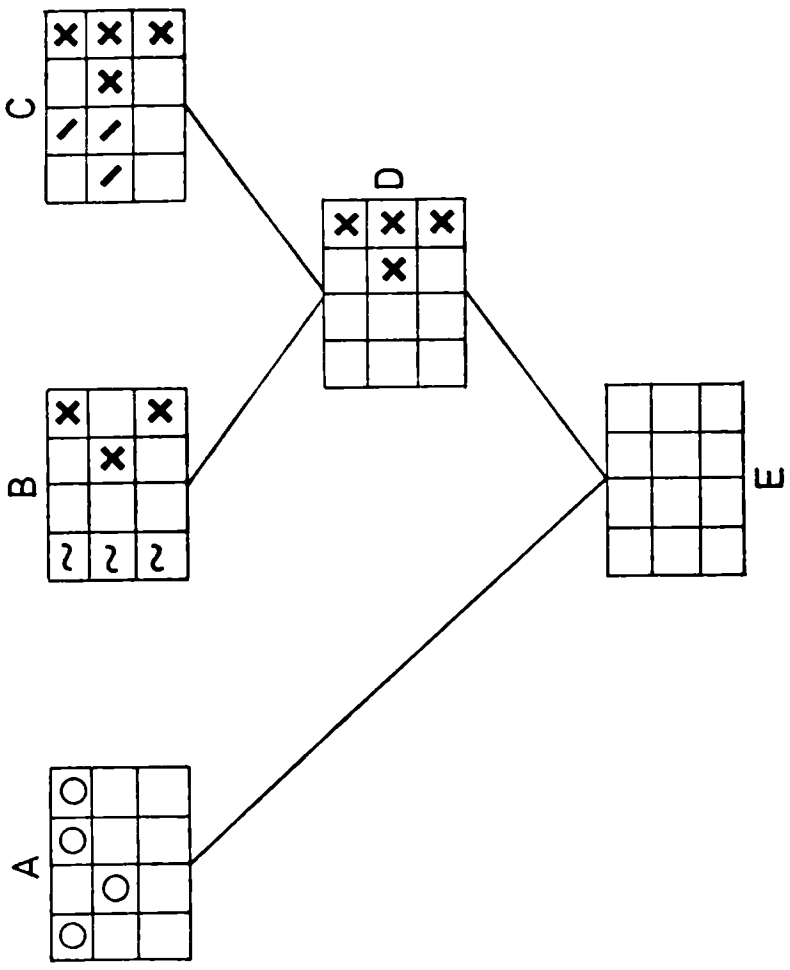

Fig. IX.5. The distinction between synapomorphic and symplesiomorphic characteristics. See text for detailed explanation.

species 'C' are autapomorphic characteristics. These characteristics are unique to species 'B' and species 'C' respectively and are of no use in establishing phylogenetic relationships because they have evolved subsequent to the common ancestor of these species.

Although cladistics are a logical means by which to reconstruct patterns of morphological and phylogenetical affinity, it is difficult to apply in practice. There are two major problems in the application of cladistics. The first is in the distinction of synplesiomorphic from synapomorphic characteristics. This distinction involves the assumption that a particular manifestation of a characteristic represents the ancestral form, and other manifestations of the characteristic are developed from it. For example, if molar tooth structure is the characteristic under analysis, and its manifestations are the tritubercular, tribosphenic and quadritubercular, it would be logical to choose the tritubercular molar as the ancestral type. The tritubercular tooth is simple in its morphology and would provide a structural basis for the development of the other patterns. There are no hard and fast rules by which the distinction between primitive and derived manifestations of a characteristic can be made. It is generally agreed, however, that fossil specimens cannot be assumed to possess primitive characteristics merely by virtue of their age. There is no reason to assume that they have not undergone evolution in a highly specialised direction. Depending on the particular morphological characteristic under analyses any one of the following criteria have been employed to make the distinction between its primitive and derived manifestations. (1) structural simplicity vs. structural complexity,(2) frequency of occurrence, (3) ontogeny.

The second problem in the application of cladistics is parallelism. A parallelism is a characteristic which has developed independently in two lineages, i.e. the last common ancestor of the two lineages did not itself possess the particular manifestation of the characteristic. Because cladistic analysis is based on the assumption that identical characteristics indicate

common ancestry, it is impossible to correct for the effects of parallelism if only one characteristic is used as the basis of analysis.

The ideal approach to cladistic analysis, to correct both for the effects of the problems involved in determining the polarity of the morphocline and the problems of parallelism, is to base the analysis on the maximum number of characteristics possible. Cladograms based on individual characteristics can be compared and the branching patterns common to the majority can be accepted as a reflection of morphological affinity and of phylogenetic affinity between the animals concerned. Those that deviate from the relationships shown by the majority can then be examined in greater detail for the effects of parallelism and problems of determining the polarity of the morphocline.

Such a cladistic analysis has been carried out for the catarrhine primates by Delson (1975), primarily on the basis of dental and cranial characteristics. His results for Cercopithecidae are presented in Fig. IX.6 and Fig. IX.7 . Fig. IX.6 includes both fossil and extant species and Fig. IX.7 includes only extant species. The branching patterns in these cladograms can be used to deduce the primitive intermembral proportions characteristic of the last common ancestor of these primates. This can be achieved by the application of the following principals.

1. The intermembral proportions of a given branching point, or node, on the cladogram are determined by the limb proportions characteristic of the component genera.
2. When more than one pattern of intermembral proportions is characteristic of the component genera, the limb proportions characterising that node are ambiguous.
3. Where ambiguity characterises one node, the morphology of the next descendent node is defined by the intermembral relationships characterising the sister group (that lineage which makes up the alternative branch from a given node) if

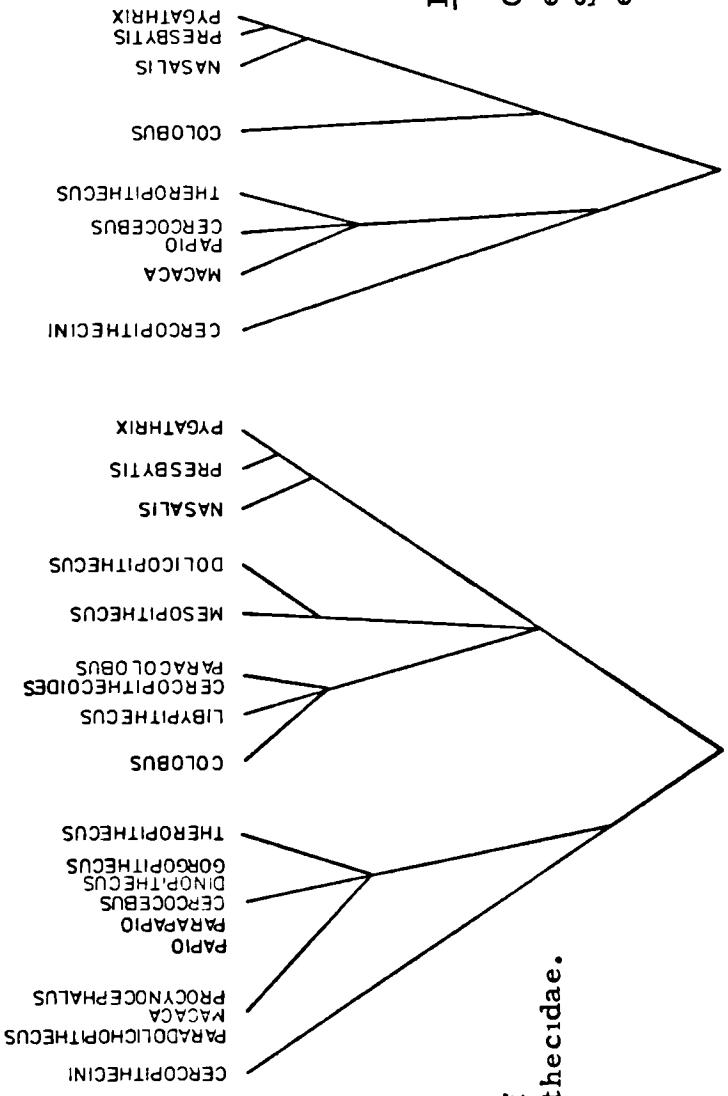

Fig. IX.6. Cladistic relationships of extant and fossil Cercopithecidae. See text for detailed explanation.

Fig. IX.7. Cladistic relationships of extant Cercopithecidae. See text for detailed explanation.

a) The intermembral proportions of the sister group are homogenous.

b) The intermembral proportions of the sister group represents one of the choices in intermembral proportions of the ambiguous node.

These principles provide the most parsimonious means of determining the sequence of intermembral alternations characterising the evolution of the cercopithecid primates and of determining the intermembral proportions characteristic of the last common ancestor of these primates.

Figs.IX.8 and IX.9 illustrate the application of these principles to the cercopithecids. In both Figures, 'E' represents a forelimb of approximately equal length to the hindlimb, and 'S' represents the condition where the forelimb is considerably shorter than the hindlimb. In Fig. IX.9, which incorporates only the extant cercopithecid primates, the morphology of the last common ancestor is ambiguous. The ancestral morphology could equally well have been a forelimb equal in length to the hindlimb, or a forelimb which was short in relation to the hindlimb. However, in Fig. IX.8, which includes not only the extant cercopithecids, but also the extinct cercopithecids, for which there is relevant information, the intermembral proportions characterising the morphology of the last common ancestor are clearly a forelimb equal in length to the hindlimb.

The conclusion that the ancestral intermembral proportions in the cercopithecids are a forelimb of equal length to the hindlimb is based on the fossil primates for which there is sufficient information as well as on the currently accepted branching patterns in the cercopithecid cladogram. Although new fossil information, as well as alternations in the position of the branching points for the extant primated based on future analysis may produce alternations in the conclusions, the present hypothesis that the ancestral pattern of limb proportions was a forelimb of equal length to the hindlimb has interesting implication for the evolution of the cercopithecid primates when combined with paleocological data.

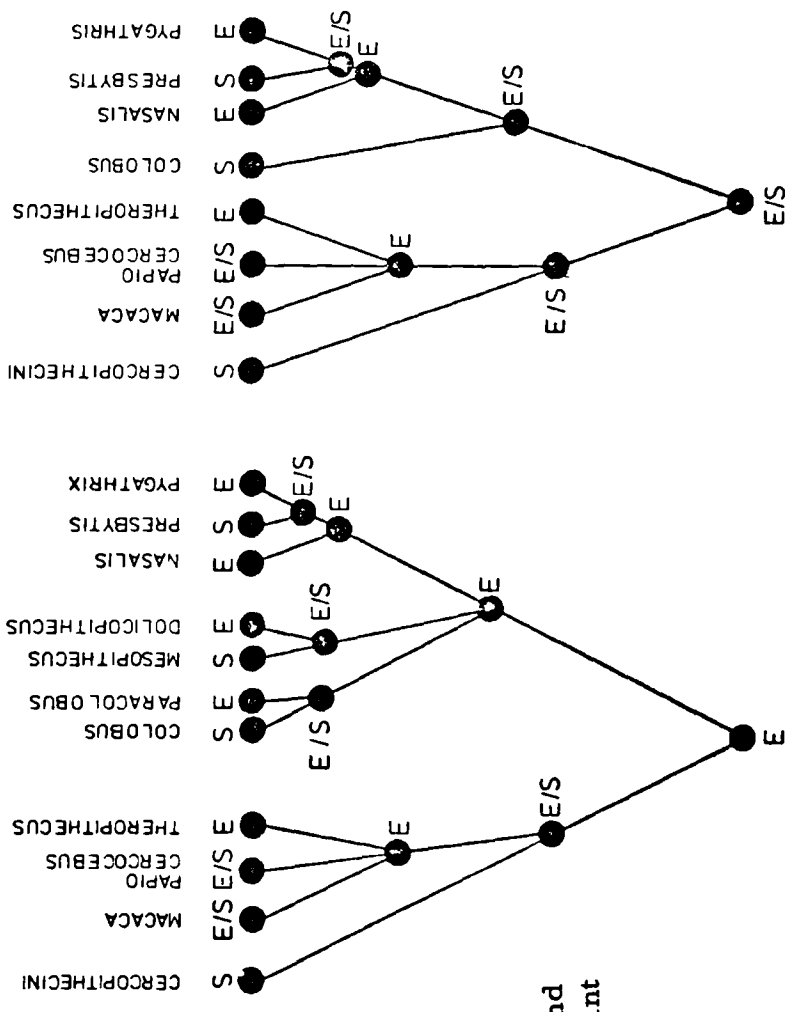

Fig. IX.8.

Intermembral proportions and the cladistic analysis of extant and fossil Cercopithecidae. See text for detailed explanation.

Fig. IX.9.

Intermembral proportions and the cladistic analysis of extant Cercopithecidae. See text for detailed explanation.

Recently Andrews(press)has carried out a cladistic analysis of the environments of extant and fossil cercopithecid primates. This analysis is based on the same principles used here to reconstruct the ancestral intermembral proportions. Andrews concludes that the ancestral environment for the cercopithecid primates was an open country, savannah environment.

The discussion in Section IX, 8 has outlined the advantages of a forelimb length equal to the length of the hindlimb in a terrestrial environment. From this, it follows that the equal length of the forelimbs and the hindlimbs in the ancestral cercopithecid would have produced a locomotorally effeicient p imate in the ancestral terrestrial niche.

The association of the equal length of the forelimbs and the hindlimbs with a terrestrial adaptation in the ancestral cercopithecid poses a number of interesting questions in relation to cercopithecid evolution and the evolution of the above branch feeding adaptation..

1. To what extent did the ancestral terrestrial adaptation affect subsequent locomotor adaptations in the cercopithecids?
2. To what extent was the primate immediately antecedent to the common ancestor of the cercopithecids preadapted to the terrestrial niche?
3. What were the ecological circumstances which surrounded the development of the terrestrial adaptation in the ancestral cercopithecid?

The first two questions can be approached through morphological analysis of extant and fossil primates. The third question is one of paleocology. The analyses presented here, as well as analyses in the current literature, are insufficient to provide a full answer to any of these questions. However, the integration of currently available information can provide a framework for future work relevant to each of these questions.

IX. 21. The Extent to which the Ancestral Terrestrial Adaptation Effected Subsequent Locomotor Adaptations in the Cercopithecids

The cercopithecids are characterised by an above branch level surface feeding adaptation as well as an apparent weight maximum in the arboreal niche of approximately 20,000 - 25,000 grams. It has previously been suggested that the absence of significant lateral mobility in the joints of these primates, particularly the forelimb and shoulder joints, and to a lesser degree, the hindlimb joints, prohibit these primates from assuming what might be termed gymnastic postures. These postures would allow the primate to distribute its weight between a number of supports. A primate that moved in such a fashion would provide itself with a large area of weight support. This would counteract the problem of a relatively high centre of gravity and a small platform of support if the primate moved primarily on top of the branches with its four limbs placed directly under the body.

Before the question of the extent to which the ancestral terrestrial adaptations effected subsequent locomotor adaptations in the cercopithecids can be satisfactorily answered, there is a major area of research which must be undertaken. Firstly, the limb and joint morphology of the cercopithecid common ancestor must be established. The analyses of cercopithecid postcrania currently in the literature have been carried out for purposes other than the reconstruction of the ancestral morphotype. For this reason there are presently no comprehensive data base upon which to reconstruct such an ancestral morphotype. This is an important area for future research. Secondly, once the ancestral cercopithecid morphotype is established, it must be shown to be synapormorphic for the cercopithecids in relation to a more remote arboreal primate ancestor. This problem could be approached through the comparison of the ancestral morphotype of the cercopithecids to the postcranial morphology of other primate sub-families, the Hominoidea, Ceboidea and the various prosimian subfamilies. Of particular interest would

be the Ceboidea comparison. Not only are members of this subfamily characterised by the limb proportions characteristic of both the above and below branch adaptations, but also there is no indication of any type of terrestrial adaptations within this group. In addition, this group is characterised by a lower average body size range than are the Old World higher primates.

Neither the post cranial morphology nor the locomotor behaviours of these New World primates are known in the detail of the Old World primates. However, if the morphology of Cebus corresponds to that of the hypothesized common ancestor of the cercopithecids, as do the limb proportions of this primate, it would be difficult to support the hypothesis that the morphology of the ancestral cercopithecid was determined by a terrestrial adaptation and that this adaptation moulded the locomotor behaviour exhibited in extant cercopithecids.

If the characteristicsof Cebus are shown to correspond with those of the ancestral morphotype of the cercopithecids, this would suggest that these characteristics developed in an arboreal niche rather than in a terrestrial niche. However, it would not necessarily negate the hypothesis that the cercopithecids passed through a terrestrial phase in their evolutionary development. Limb proportions and post cranial morphology developed at a small body size in an arboreal environment could have preadapted the cercopithecids to a terrestrial existence. In this environment body size could have increased and recolonisation of the arboreal environment would then result in a relatively large bodied arboreal population of primates.

It is interesting that although both patterns of limb proportions are present in the New World Medium Sized primates, this does not occur in the larger size ranges equivalent to Lagothrix, Brachyteles, Ateles and Alouatta. This is, perhaps, not an unrelated problem to that of the evolution of the modern cercopithecid and the hypothesized terrestrial adaptation.

IX. 22. The Below Branch Adaptation and the Evolution of the Hominoidea

Before the 1950's and the discovery and publication of the fossil primate postcranial material from the Miocene of East Africa, the most widely accepted hypothesis for the locomotor ancestory of the Hominoidea was one of brachiation. The last common ancestor of the pongids and man was variously interpreted as a large bodied ape similar in postcranial morphology to the extant pongids (Keith 1899-1934, Gregroy 1916-1949, among others) or a small bodied brachiating ape (Morton 1922-1935, Schultz 1927a, 1927b, 1930, 1936, 1969, among others). If the features shared by the hominoids are interpreted as resulting from a common brachiating ancestry, none of the known Miocene fossils can be considered to represent the locomotor type of the last common ancestor of this radiation. However, the literature review (Chapter II) and the discussion in Chapter IX have suggested that the below branch feeding adaptation and the morphological features associated with this adaptation would have provided the prerequist morphology for the subsequent evolution of the acrobatic brachiation of the gibbons, the knuckle walking and quadrumanual locomotion of the large bodied pongids and the bipedal locomotion of Homo. The emerging picture shows that these modern hominoids are the highly specialized decendents of a prolific Miocene radiation based on the below branch feeding morphology. The demise of this radiation has recently been explained in terms of competition between the se Miocene hominoids a and the evolving monkeys. Andrews (press)has suggested that the key feature in relation to the success of the monkeys, and the demise of the Miocene hominoids, was the evolution of the ability in the monkeys to digest toxic food substances. In particular, the ability of the monkeys to digest tanin (Wrangham 1980) would allow them to eat unripe fruits. If the availability of ripe fruits was a limiting factor for the Miocene hominoids the

ability of the Miocene monkeys to exploit the fruit crop in advance of the hominoids could have been a crucial feature in the decline of the hominoids. This model would obviously apply only to those areas where fruit was the primary food source for the hominoids. Much of the evidence of the Middle Miocene hominoids comes from Eurasia and much of it is associated with savannah woodland environments (Andrews 1981). It is not clear to what extent this dietary hypothesis would apply to these Eurasian environments. However it is clear from the geological record that as the Miocene progressed the environment in Eurasia became increasingly arid. In association with this the primate fauna, both hominoid and monkey, decreases and finally disappears from the record approximately 8 million years ago. It is probable that the demise of the hominoid radiation is associated not only with the dietary competition between the monkeys and apes which would have operated throughout the distribution of the two families, but also with the climatic change in the Late Miocene which would have rendered a good percentage of the geographical range of the late Miocene primates uninhabitable to them.

Within this framework, the surviving hominoids can be viewed in terms of the behavioural specializations that allowed them to successfully compete with the monkeys in the late Miocene, Pliocene and Pleistocene. In this context, the acrobatic brachiation of the gibbons and siamangs can be interpreted as an efficient means to reach fruit growing in the terminal branch position in the trees. Monkeys would be restricted in their exploitation of such fruit by virtue of their above branch locomotor pattern. The large bodied pongids would be distinguished by their size in an arboreal or semi-arboreal forest niche.

The allometric analyses presented here have shown that the arboreal Od World monekys (the Branch Sitting and Walking

primates and the Old World Semibrachiating primates) are, with the exception of the male Nasalis, restricted to body weights below 10,000 grams. The male Nasalis is equivalent in body weight to the larger primates in the Part Ground Standing and Part Branch Sitting and Walking group and the Ground Standing and Walking group. This is considerably below the weight range of the extant pongids (37,750 - 136,680 grams). Within the Old World monkeys there is a trend toward increasing terrestriality with increasing body weight (Section IX.8). It has been suggested here that the morphological features of the forelimb in these primates that emphasize stability at the expense of mobility. The lack of mobility in the forelimb would restrict body weight in the arboreal niche for these primates. This would result from the inability of these primates to spread their body weight between a number of supports in the arboreal niche and, therefore, overcome the problem of large body size in relation to the strength of a single support.

In Homo sapiens, the evolution of bipedality and the resulting freedom of the forelimb from locomtor function, the development of hunting behaviour, economic division of labour, food sharing and the development of cultural behaviour resulted not only in a successful adaptation to a savannah or dry country environment but also in an ecological adaptation different from that of the savannah adapted Old World monkeys.

The extent to which this model of hominoid evolution can be accepted depends upon a number of factors. Prime among these is the degree to which the model of ecological competition between the monkeys and apes in the Miocene can be shown to be correct. In connection with this is the extent to which the adaptations of the extant hominoids removes them from ecological competition with sympatric monkey species. These adaptations involve not only locomotor and dietary adaptations, but also social organization and specific means of exploiting the available resources. In addition, it is necessary to know the degree to which the below

branch feeding adaptations would provide the prerequist morphology for the specialized locomotor patterns observed in the extant hominoids. Also it is important to ascertain the degree to which those morphological features which are shared by the extant hominoids, and cannot be attributed to the generalized below branch feeding common ancestor, can be attributed to parallel development in these lineages subsequent to the divergence of the lineages leading to the modern hominoids. These are all points that deserve further research.

IX. 23. Locomotor Evolution in the Hominidae

The earliest undisputed evidence for bipedal locomotion in the Hominidae dates from between 3.6 and 3.75 million years old and comes from the Tanzanian site of Laetoli. Although there are no postcranial bones among these fossils, the discovery of clearly preserved footprints at this site proves beyond a shadow of a doubt that there were hominids at this time that moved with a perfected bipedal locomotion. Outside of a small fragment of a hominid distal humerus from the site of K anapoi (4 -4.5 million years old, Patterson and Howells, 1967) the earliest postcranial bones from a Pliocene hominid come from the Ethiopian site of Hadar (3.3 - 2.8 million years old, Johanson and White, 1979). The most famous of the Hadar fossils is Al-288-1, an associated skeleton with approximately 40%of the bones preserved. The analysis of the form of the knee joint and pelvis of this skeleton as well as other postcranial fragments suggest that hominids of this time were anatomically adapted to bipedal locomotion (Johanson and White, 1979). Although there are no similarily complete hominid skeletons from later Plio-Pleistocene hominids, isolated postcranial bones suggest that there are two distinct postcranial morphologies among these fossils, both adapted to bipedal locomotion (Day, 1978). One is characteristic of the australopithecines, both the robust and the gracile species, and the other is characteristic of early Homo.

The literature review in Chapter II has shown that there is a body of inferential evidence that suggests that there may be also two patterns of limb proportions among these hominids (Genet-Varchin, 1966, Coon, 1962, Robinson, 1972, Helmuth, 1968, Hamilton, 1972, McHenry, 1974, 1978). In the most recent analysis McHenry (1978) has recognized the two proportional patterns among four published associated hominid skeletons, three from Koobi Fora (KNM-ER-803, KNM-ER-1500 and KNM-ER-1503/1504) and the Al-288-1 skeleton from Hadar.

He interprets the KNM-ER-803 skeleton to have postcranial proportions similar to modern Homo sapiens in the indices that can be measured on these fragmentary remains. These indices include the sum of the ulnar anterior-posterior transverse diameter of the shaft taken just distal to the ulnar tuberosity, the sum of the femur anterior-posterior shaft diameter taken just distal to the lesser trochanter and indices based on estimated long bone lengths (Section II. 5). The second pattern illustrated by the remaining three skeletons is similar to Homo sapiens in the comparison of some indices and similar to the pongids in others, however comparsion of reconstructed long bone lengths points toward the conclusion that these hominids had a longer forelimb than hindlimb. The conclusion that at least some of the Plio-Pleistocene hominids were characterised by a longer forelimb than hindlimb is also consistent with suggestions made by Leakey (1971) on the basis of the long and robust KNM-ER-739 humerus, by Howell and Wood (1971) on the basis of the long ulna from the Omo and by McHenry (1974) on the basis of the associated distal humerus and talus from Kromdraai.

These authors, as well as Johanson and White (1976), imply that the limb proportions observed in modern Homo sapiens and in the KNM-ER-803 skeleton developed by a progressive reduction in the length of the forelimb in relation to the length of the hindlimb from an ancestral condition seen in A1-288-1, KNM-ER-1500, KNM-ER-1503/1504 and TM-1517 (the associated humerus and talus from Kromdraai). There is, however, no evidence for this interpretation of the ancestral hominid limb proportions other than the long held subjective opinion that hominid ancestors were brachiators and that long forelimbs relative to hindlimbs are associated with this form of locomotion (Section IX. 22.).

The allometric analysis of limb and bone proportions in primates in general and in hominids in particular is relevant to three points in this argument. Firstly, allometric analysis is relevant to the reconstruction of the limb proportions and

locomotor pattern of the last common ancestor of the hominids and pongids. Secondly, it is relevant to the interpretation of the limb proportions of the fossil hominids in relation to the proportions of the common ancestor, and the extant hominoids, and, thirdly, it is relevant to the question of the existance of two separate proportional patterns in the fossil hominids when body size is taken into account. These points will be taken in turn.

23.a. Limb and Bone Proportions of the Last Common Ancestor of the Hominids and the Pongids

The allometric analysis of the limb and bone proportions of the extant and fossil higher primates has supported the theory that the ancestral hominoid locomotor pattern involved a below branch or climbing adaptation rather than a brachiating locomotor adaptation (Sections IX.9, IX.10, IX.11, IX.15, IX.18). It has been suggested also that a forelimb of approximately equal length to the hindlimb, and particularly a humerus of approximately equal length to the femur, as found in the modern genera Alouatta and Lagothrix, would be the likely proportional pattern of the ancestral climbing hominoid (Sections IX.9, IX.11). Together with these proportions a low brachial index would also characterise the ancestral pattern (Section IX.10).

This concept of the ancestral hominoid is supported by evidence from the comparative morphology of modern primates, the comparative analysis of the locomotor patterns of modern hominoids as well as the comparison of the morphology of fossil hominoids with the morphology of modern primates engaged in climbing locomotion (Section IX.22). Such a generalised common ancestor, adapted to a climbing form of locomotion, would also be ideally preadapted for the development of bipedal locomotion, and moreso than any of the extant Old World primates (Section IX.16). Cartmill and Milton (1977) have ennumerated a series of

preadaptations for orthograde posture characterising not only the extant hominoids including Homo sapiens, but also the extant climbing New World Semibrachiators and the lorisines. These preadaptations are associated with a locomotor pattern of slow suspensory quadrupedalism, or what has been termed climbing by Stern (1976) and Tuttle (1976). In addition, Stern (1971) has pointed out the close similarity in the hindlimb musculature of Homo sapiens and the New World climbing primate Alouatta. Arguing from the points raised in Section IX.16 in relation to the energetics of both quadrupedal and bipedal locomotion in primates in general, and in relatively large bodied primates in particular, it is likely that bipedalism would be a form of locomotion as efficient as quadrupedalism in generalized primates with the preadaptations resulting from a climbing ancestry. Although the specific pressures resulting in the development of bipedalism in the human line are not known, it can be concluded that the generalised common ancestor, as well as the Miocene hominoids such as Proconsul, Paidopithex, and Austriacopithecus would have been better preadapted to the development of this form of locomotion than are any of the extant non-human Old World primates. An early commitment to terrestrial quadrupedal locomotion in the Old World monkeys and the resulting preclusion from the development of the necessary skeletal and visceral preadaptions for orthograde posture resulting from a climbing locomotor ancestry has eliminated the possibility of the development of bipedalism in this group. The increase in body size in the extant pongids and the resulting reduction of the length of the hindlimb in relation to body size (Section IX.11) has also reduced the possibility of the development of efficient bipedalism in this group.

Therefore, the allometric analysis of the limb and bone proportions in the higher primates, coupled with other work in comparative morphology has provided a different picture of the

last common ancestor than the traditionally accepted brachiating ancestor with very long forelimbs in relation to its hindlimbs.

23.b. The Limb Proportions of the Fossil Hominids

The A1-288-1 skeleton is the earliest of the hominid fossil postcranial material that is complete enough to include in the allometric analyses. The relationship between the length of the femur and the length of the humerus in this skeleton clearly shows the primitive pattern of the reconstructed last common ancestor (Section VII.6). A1-288-1 deviates from the allometric relationship characterising the Branch Sitting and Walking primates to the same degree as do the New World climbing primates. This skeleton does not show the short femur in relation to humerus length of the extant large bodied pongids. The necessary measurements of the cross section of the femur required to infer body weight for A1-288-1 are not available, however body weight can be inferred from the length of the humerus (Chapter VIII). The comparison between body weight inferred from this parameter and the length of the femur (Fig. IX.9) shows the expected relationship observed in all of the higher primates, including modern Homo sapiens, with the exception of the large bodied, short legged pongids. Therefore, A1-288-1 is not pongid-like in its humero-femoral relationship but is similar to the inferred ancestral pattern.

The brachial proportions of the A1-288-1 skeleton also are close to the inferred primitive pattern, if the isometric hypothesis of brachial increase in the higher primates is accepted (Section VII.7). However, if the alternative hypothesis of brachial increase is accepted, a positively allometric increase of the length of the radius in relation to the length of the humerus, the A1-288-1 skeleton would show a specialised, or derived, reduction in the length of the radius in relation to the length of the humerus. A short radius in relation to the length of the humerus is a pattern seen also in both modern Homo sapiens and the extant Gorilla (Section V.10).

It is important to emphasize that there is no evidence in the long bone proportions of Al-288-1, other than a possible reduction in the length of the radius in relation to the length of the humerus, of any specialisation from the inferred primitive pattern. If the hypothesis of a climbing ancestry for the Hominidae is accepted, this would imply that the hominid ancestor left the climbing locomotor adaptation at a body size below that which would necessitate the reduction of the length of the hindlimbs observed in the large-bodied pongids. It is interesting to note in this context that the inferred weight for the Al-288-1 skeleton is considerably below that of the chimpanzee, the smallest bodied of the extant pongids that show reduction of the length of the hindlimb in relation to the length of the forelimb.

Subsequent hominid postcranial material from the Plio-Pleistocene is limited. The fragmentary KNM-ER-1503/1504 skeleton assigned to the genus Australopithecus has been interpreted by McHenry (1978) to have long forelimbs in relation to hindlimbs and, therefore, to be more like the pongids in its limb proportions than like Homo. However, comparison of the reconstructed lengths of the humerus and of the femur do not support this interpretation. McHenry reconstructed the length of the humerus on the basis of the biepicondylar width and the trochla to midepicondylar distance. Using both a Pan comparative sample and a modern Homo comparative sample, the reconstructed lengths were almost identical, thus confirming the similarity in the proportions of the humerus in both Pan and in Homo. This reconstructed length is considered to be accurate in this analysis. The total length of the femur is more problematical. McHenry reconstructed the total length of the femur from measurements of the proximal end of the femur. Not only is the proximal end of the femur unique in shape in the australopithecines (Day, 1978), but the length of the femur relative to the proximal end is considerably different in Pan and in Homo (McHenry, 1978). McHenry's projections on both of these samples produce very different reconstructed femur

lengths. However, when both of these lengths are compared to the reconstructed humerus length, this skeleton falls midway between the position of modern Homo and the extant pongids (Section VII. 6). From this it can be concluded that KNM-ER-1503/1504 shows neither the relatively short humerus length in relation to femur length observed in extant Homo nor the relatively short femur length in relation to the length of the humerus of the extant pongids. The range covered by the KNM-ER-1503/1504 skeleton in this relationship spans both the isometric projection of proportions from the A1-288-1 skeleton, as well as the positive allometric increase from this skeleton. On the basis of this evidence, the hypothesis that KNM-ER-1503/1504 maintains the primitive relationship between humerus length and femur length cannot be rejected. It is possible, therefore, that the humerus length and the femur length of KNM-ER-1503/1504 represents simply a scaled up version of the proportions observed in the A1-288-1 skeleton. This conclusion, however, is based on the questionable reconstruction of the length of the femur of KNM-ER-1503/1504.

There is some evidence presented by Walker (1973) that might suggest that the robust australopithecines were characterised by a reduced length of the femur (hindlimb) in relation to both body weight and to the length of the forelimb. If this were true it would negate the above conclusion and indicate a specialisation of the postcranial skeleton of these hominids. The Walker reconstruction of the robust australopithecine femur produces a more robust femur than that found in the Cercopithecini or in Homo but less robust than that of the extant pongids (Section VII. 3). This would indicate a reduction in the length of the femur and the hindlimb from the primitive condition. A composite reconstruction such as Walker's is not conclusive evidence for a reduction in femur length. However the hypothesis of a reduced hindlimb is supported by a series of ratios taken on fragments

of the forelimb and the hindlimb bones of KNM-ER-1500 and on the comparison of the distal humerus and talus of TM-1518 (McHenry, 1974, 1978). These ratios show proportions within the range of the extant pongids or midway between the ranges of the pongids and the hominids. A conclusive decision in relation to the specialisation of the proportions shown by this material cannot be made until the similar measurements are made on the Al-288-1 skeleton. However, on the basis of this analysis it is possible that these hominids were characterised by limb proportions different from the inferred primitive condition observed in Al-288-1.

There is also interesting suggestive evidence that the forelimb of the robust australopithecines was long in relation to the condition observed in the Al-288-1 skeleton. The complete ulna from the Omo is absolutely as long as that of a female Pongo and completely outside the range of variation in modern Homo sapiens. If this ulna were combined with a humerus of the length to produce the brachial proportions observed in either Al-288-1 or in modern Homo sapiens, the resulting limb would indicate an individual of gigantic stature. If this ulna is combined with one of the largest and most robust australopithecine humeri available (KNM-ER-739) the resulting brachial proportions are similar to Pan and are consistant with an isometric increase from the proportions observed in Proconsul africanus and inferred to be the primitive hominoid, as well as Catarrhini, condition. Such a composite forelimb is again weakevidence upon which to suggest that the australopithecines were characterised by the primitive brachial proportions, however, the ulna itself is strong evidence upon which to support the hypothesis of at least two different brachial proportions among the hominids of the Plio-Pleistocene.

It is thus possible that the robust australopithecines were specialised in having a short femur for their humerus lengths

while maintaining the condition of a relatively high brachial index. Both of these conditions would indicate fundamentally different adaptations than those inferred for the A1-288-1 skeleton. The short femur (hindlimb) for the length of the humerus has been explained in relation to a relatively large body size in either an arboreal environment or in a terrestrial environment. Section IX.11 has discussed the pressures for hindlimb reduction in both of these locomotor circumstances. The relatively high brachial index is best interpreted in relation to the reduced brachial proportions in A1-288-1. If this reduction occurred in response to manipulative efficiency (Tuttle and Basmajian, 1974, Keith, 1926) it would be logical to suggest that A1-288-1 had a greater degree of manipulative skill, or tool using ability, than did the robust australopithecines. Both of these points are highly speculative. However, if future fossil material supports the suggestion that the robust australopithecines were characterised by a reduced femur (hindlimb) length and a higher brachial index than the A1-288-1 skeleton, the A1-288-1 skeleton would necessarily be precluded as a direct ancestor of the robust australopithecines. In relation to the reduced hindlimb length in the robust forms, if the A1-288-1 skeleton were already bipedal as suggested here, the maintenance of the primitive relatively long hindlimb would in subsequent bipedal hominids be a necessary prerequiste to bipedal efficiency in terms of speed and stride length. There would be no apparent pressure for hindlimb reduction in subsequent forms. In relation to the apparent specialised reduction in the length of the radius in relation to the length of the humerus in A1-288-1, and the inferred manipulative efficiency of such a reduction, it would be difficult to accept a redevelopment of a longer radius in a descendant popualtion. At present there appear to be no apparent selective pressure which would necessitate the parallel redevelopment of the primitive pattern.

Postcranial material from the other Plio-Pleistocene hominids is too limited to include in the majority of these analyses. Australopithecus africanus is particularly difficult to discuss in this context. The STS-14 femur is too distorted and fragmentary to speculate seriously on its robusticity and, therefore, possible reduction of length in relation to body size. There is also insufficient forelimb material to speculate on the brachial proportions of this species.

In relation to the Plio-Pleistocene genus Homo (cf. Homo habilis) there is also little evidence. The limb proportions of KNM-ER- 803, a skeleton that McHenry (1978) considers to be similar to modern Homo sapiens, have not been published. The femur, KNM-ER-1481, shows no indication of unusual robusticity characteristic of hindlimb reduction. At a much larger body size, this femur shows the primitive robusticity relationships of the non-pongid higher primates.

Therefore, the main point that can be drawn from the allometric analysis of the limb proportions of the fossil hominids is the similarity of the proportions of Al-288-1 to the inferred proportions of the common hominoid ancestor engaged in a climbing form of locomotion. Unfortunately, because of the absence of associated skeletons, it is not possible at present to conclusively show that Australopithecus robustus or Australopithecus boisei are characterised by proportional relationships different from those seen in the Al-288-1 skeleton or different from the unknown proportions of Australopithecus africanus or early Homo.

IX. 24. The Relationship between Body Weight and the Size and Strength of the Cross Sections of the Limb Bones

The cross section of a bone must adapt directly to the load to which it is exposed during the locomotion of an animal. It is well established that the observed size and strength of the cross section of the bone results not only from genetic factors but also from the stress to which the bone is exposed during the life of the animal (Evans, 1957). As the result of this the assumptions which must be made in the interpretation of the allometric relationships between body weight and cross sectional size are different than those which are made in the allometric analysis of limb and bone proportions (Section IX. 4). In the case of the cross section, it is not specifically growth, but the manner in which body weight effects the load borne by the bone which is the crutical independent variable in the allometric analysis. The actual load borne by the bone is determined by body weight, locomotor pattern, limb length and the various muscular and/or ligamentous arrangements of the postcranial skeleton (Pauwels, 1965, Kummer, 1959). In addition, interpretation is complicated by uncertainity as to the manner in which the cross section of the bone adapts to the load it must bear. The cross section can adapt by alterations in the external size of the section, alterations in the cortical thickness and alterations in the shape of the cross section (Pauwels, 1965, Lovejoy et al., 1976, Currey, 1967). Therefore, although body weight does have a direct effect on the stress which the cross section must adapt, interpretation of the relationship between body weight and cross section size is made difficult by the uncertainities in both the manner in which body weight relates to the load borne by the cross section and the manner in which any single variable taken to represent cross section strength actually relates to the strength of the cross section.

With these points in mind, it is perhaps surprising that both the midshaft circumference of the humerus and the midshaft circumference of the femur show a highly correlated linear relationship with body weight across the sample (Section VI.9). However, when the midshaft circumference of the femur is compared directly to the midshaft circumference of the humerus there is considerable variation in the upper ranges of the distribution (Section VI.10). Pongo is singificantly displaced in the direction of a large humerus circumference for its femur circumference, while Homo sapiens is displaced in the opposite direction. This suggests that body weight is effecting the bones of the forelimb and the bones of the hindlimb in these primates in different fashions.

This is not a surprising conclusion in view of the bipedal locomotion in Homo sapiens and the forelimb dominated quadrumanual climbing in Pongo. What is surprising, however,, is the high correlation of these variables with each other in the smaller bodied primates. These smaller bodied primates are characterised by locomotor patterns as diverse as the highly acrobatic brachiation of the gibbons and the fully terrestrial quadrupedalism of Papio.

The use of circumference as a measure of the size of the cross section of the long bones does mask a considerable degree of variation in the shape of the cross sections, however. The circumference of the femur masks variation in shape in the pongids and in Homo sapiens in relation to the smaller bodied primates, in spite of their variable forms of locomotion. Where the smaller bodied primates have a circular cross section, the pongids, and particularly Pongo and Gorilla, have a markedly ovoid cross section with the long axis in the transverse plane. Homo sapiens has a larger sagittal diameter of the cross section than expected in the smaller bodied forms.

Where the shape of the femur shows most variation in the larger bodied primates, the shape of the humerus is most variable in the smaller bodied forms. The Branch Sitting and Walking cercopithecines have a transversely ovoid humerus while the Old World Semibrachiating primates, as well as Papio anubis and the hominoids have a humerus that is round in cross section (Section VI. 7). The variation in shape in the smaller bodied primates appears to result from variation in the transverse diameter of the cross section in relation to body weight, rather than in the sagittal diameter in relation to body weight (Sections VI. 5 and VI. 6).

The separation between the Branch Sitting and Walking primates and the Old World Semibrachiating primates is also apparent, although to a lesser degree, in the comparison between body weight and the average midshaft cortical thickness of the cross section of the humerus (Section VI. 11). The Branch Sitting and Walking primates tend to have a greater average cortical thickness in relation to body weight than do the Old World Semibrachiating primates. In relation to cortical thickness, this distinction is particularly clear in the comparison between the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus (Section VI. 12). The Branch Sitting and Walking primates have a larger average midshaft cortical thickness of the humerus for the average midshaft cortical thickness of the femur than do the Old World Semibrachiating primates.

Therefore, the consistancy of the circumference of the humerus in relation to body weight masks the non-allometric differences in the shape of the cross section of the humerus and the average midshaft cortical thickness of the humerus in these smaller bodied higher primates as does the circumference of the midshaft of the femur in the larger bodied forms. This points toward the conclusion that although the midshaft circumference of the humerus and the midshaft circumference of the femur

show a highly correlated isometric increase in relation to body weight, factors other than body weight are responsible for variation in shape and cortical thickness in the higher primates.

The allometry of the average midshaft cortical thickness of the humerus and the average midshaft cortical thickness of the femur also point to some interesting conclusions when compared to the allometry of the midshaft circumference of the humerus and the midshaft circumference of the femur (Sections IV.4 and IV.5). The average midshaft cortical thickness of the femur is significantly positively allometric in relation to the midshaft circumference of the femur while the average midshaft cortical thickness of the humerus is isometric in relation to the midshaft circumference of the humerus. The differences in the allometry of the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus are also apparent when both of these variables are compared to body weight (Section VI.11). Although both the average midshaft cortical thickness of the femur and the average midshaft cortical thickness of the humerus are positively allometric in relation to body weight, the average midshaft cortical thickness of the femur is significa tly more positive than is the average midshaft cortical thickness of the humerus. This suggests that the average midshaft cortical thickness of the femur is responding to increase in body weight in a different fashion than are the external measurements of the femur cross section or the average midshaft cortical thickness of the humerus. This may be related to the unique hindlimb dominance in the higher primates where the hindlimbs carry a greater proportion of body weight than do the forelimbs (Kimura et al., 1979). As body weight increases the hindlimbs would carry a relatively greater amount of body weight than the forelimbs.

The allometry of the area of the cross sections of the humerus and of the femur (Section VI.16) and of the section

modulus of the humerus and of the femur (Sections VI. 13 and VI. 14) reflect the conslusions of the previously discussed allometries of the other cross section measurements. The average area of the midshaft cross section of the humerus and of the femur as well as the idealised section modulus of the midshaft cross section of the humerus and of the femur are all significantly positive in relation to body weight. Therefore, the strength of the cross section as reflected by these measurements (area reflecting the strength in compression and the section modulus reflecting strength in bending) increase more rapidly than do the simple circumference measurements of the femur and of the humerus.

There is still much to learn in relation to the allometry of the size and of the strength of the cross sections of the long bones. Until the manner in which the external measurements of the bone cross section relates to the actual strength of the bone and the manner in which body weight actually effects the stress to which the bone must adapt are clarified, it is futile to suggest wide ranging theoretical hypotheses for the mechanical determinants of cross section size.

McMahon (1973) recently has suggested, within the theoretical model of elastic similarity, that no matter what the conditions of loading, whether they be by buckling, bending, torsion or a combination of these conditions, the length of a bone should be proportional to the two-thirds power of its diameter. In addition, the length of the limb should be proportional to the one quarter power of body weight and the diameter of a limb should be proportional to the three eights power of body weight. McMahon has supported his argument with emperical data from bovids and other artiodactyles (1975).

The assumptions underlying this model are that the limb is loaded by gravitational self loading and that the length of the limb times its diameter squared is proportional to body weight. Neither of these assumptions can be accepted to be true across the primates in particular or mammals in general. Alexander et al.

(1979) have recently shown that McMahon's model is not supported by emperical data for selected primates as well as for non-primate mammals as a whole. This conclusion is also confirmed by this analysis, even if the sample is restricted to primates of similar locomotor types and similar body proportions. In the arboreal Old World monkeys, the length of the forelimb and the length of the hindlimb are isometric with body weight as are the diameters as well as the circumferences of the midshafts of the bones. The direct comparison of the circumference of the midshaft of the femur and the length of the femur is the only relationship that deviates from isometry, and this deviation is in the direction opposite to that predicted by McMahon.

These data also contradict the work of Preuschoft and Weiman (1973). These authors suggest that as body size increases the cross section of the bone will become relatively smaller. Their analysis is orientated towards the hypothesis that gracile limb bones and particularly gracile forelimb bones in primates do not necessarily indicate a change in function from a quadrupedal form of locomotion to an armswinging or brachiating locomotor pattern. The assumption underlying this model is that limb bones are loaded in bending during locomotion and that the diameter of the cross section is proportional to the second moment of inertia of the section, and, therefore, proportion to body weight to the fourth power (Section II.2). Therefore, the strength of the cross section in bending increases more rapidly than does body weight. In order to maintain physiological similarity (identity of strength) a larger animal can have a more gracile cross section in relation to body weight than a smaller animal.

Both of these models are simplistic in their assumptions in view of the complex variables involved in both the loading of the cross section and in the response of the cross section to the stress

it must bear. Simple allometric analysis of body weight, cortical thickness, external size and shape of the cross section and limb length can establish that these models do not correspond to emperical data. However, these allometric analyses can do no more than offer a framework for the more detailed study of bone robusticity and the reaction of the bone cross section to stress.

X. Conclusion

X. Conclusion

In conclusion, evidence from the allometry of the length of the long bones and of the size, shape and strength of the midshaft cross section of the long bones in higher primates supports the following hypotheses in relation to the evolution of primate locomotion.

1. The primitive post cranial proportions of the higher primates were similar to those found in the extant New World Semibrachiators, Alouatta and Lagothrix. The forelimbs and the hindlimbs were of approximately equal length and the humerus made up a greater proportion of the total forelimb length than did the radius.
2. The extant Old World Monkeys experienced an early phase of terrestrial, or semiterrestrial, locomotion in their evolutionary history.
3. The remaining Old World primates, the ancestral Hominoidea, retained the primitive post cranial proportions as well as the below branch, or climbing, locomotor niche. As body size increased to the extremes seen in the modern pongids, there was an alteration in limb proportions involving, in particular, the reduction in length of the hindlimb in relation to body weight. This reduction in the length of the hindlimb equally can be explained as a response to body size increase in a below branch arboreal niche or in a terrestrial niche. There is no indication of a specialized reduction in the length of the hindlimb in the available Miocene hominoid fossil material. On present evidence this would suggest that these forms did not reach the body size that would necessitate reduction in the hindlimb length in order to facilitate locomotion.
4. The ancestral hylobatids specialised in a greater amount of below branch, or suspensory behaviour than is characteristic of the other below branch primates of their general body size. They show an unusually lengthened forelimb in relation to their body weight as well as a lengthened hindlimb. Their specific skeletal

and locomotor adaptation most likely occurred in response to the radiation of small bodied monkeys in the Miocene. However, none of the known Miocene hominoids show any indication of the proportional specializations characterising the extant hylobatids and their brachiating form of locomotion.

5. The last common ancestor of the pongids and the hominids remained in the below branch niche to a larger body size than observed in extant Alouatta and Lagothrix, but not to the body size requiring the specialised reduction of the hindlimb that is found in the extant pongids. There is no evidence to suggest that a short hindlimb in relation to body weight was ever a characteristic of the hominid line.

6. There are also no groups upon which to suggest that an unusually long forelimb, or the brachiating locomotor pattern traditionally associated with this feature, played any part whatsoever in hominoid evolution. In this context some of the Plio-Pleistocene hominids correspond closely to the primitive postcranial proportions suggested not only for the ancestral hominoid but also for the ancestral higher primate. Australopithecus afarensis corresponds closely to the suggested primitive pattern with a possible specialisation in the reduction of the length of the radius in relation to the length of the humerus.

7. Based on present fossil evidence, it is not possible to determine conclusively the limb proportions of the other species of Plio-Pleistocene hominids. However, there is some fossil evidence that might suggest that the robust australopithecines (Australopithecus robustus and Australopithecus boisei) had a reduced hindlimb in relation to body weight in addition to a relatively long radius in relation to the length of the humerus. If this is ultimately proven to be the case, it would indicate that these hominids experienced a different locomotor history than did the hominids in the line leading to Australopithecus afarensis.

Based on the allometric analyses, these suggested robust australopithecine limb proportions would best be explained by the hypothesis that the ancestors of these hominids remained in an arboreal niche to a larger body size than did the hominids in the line leading to Australopithecus afarensis. There is also little evidence upon which to establish the postcranial proportions of members of either the species Australopithecus africanus or Homo sp. (cf. Homo habilis). However, the robusticity of the femur of early Homo is identical to that of modern Homo sapiens.

8. Modern Homo sapiens is similar in postcranial proportions to Australopithecus afarensis (Al-288-1). However modern Homo sapiens has a marginly longer hindlimb in relation to its forelimb length than does A. afarensis. It is not clear whether this results from a longer hindlimb in relation to body weight or from a shorter forelimb in relation to body weight in Homo sapiens in relation to Australopithecus afarensis.

More specific conclusions emerging from the allometric analyses are the following

1. Trunk length is not an accurate measurement of body weight across the higher primate sample. The most efficient measurement for the prediction of body weight in extant and fossil higher primates is the transverse diameter of the midshaft of the femur. Other suitable measurements are the circumference of the midshaft of the femur and the length of the humerus.
2. External measurements of the size and shape of the cross section of a long bone are not accurate measures of the strength of the cross section. Strength, as measured by the idealised midshaft area of the cross section or by the idealised section modulus of the cross section, increases more rapidly in relation to body weight than do the external measurements of the cross section.
3. The average midshaft cortical thickness of the femur responds to increase in body weight in a different fashion than do the

external measurements of the cross section of the femur or the cortical thickness of the humerus. This may be related to the unique hindlimb dominance in the higher primates where the hindlimb carries a greater proportion of the body weight than does the forelimb. As body weight increases the hindlimb would carry a relatively greater amount of body weight than the forelimb.

4. Both body weight and locomotor pattern play a role in determining the external size and shape of the cross section of the long bones.

The allometric analyses of the cortical thickness and of the external size, shape and strength of the cross section of the long bones are intended only to establish the general allometric nature of these variables in relation to body weight. They are best viewed as providing a framework for further study of the bone robusticity and of the reaction of the bone cross section to stress. Such further analyses would most fruitfully be accomplished through the application of computed tomography and of experimental stress and strain analysis on the cross sections of the limb bones in conjunction with detailed biomechanical analysis of the forces to which the bone is subjected during locomotion.

In relation to the hypotheses of the evolution of locomotion in the higher primates, this analysis has left a number of unanswered questions that are suggested as fruitful areas in need of further study.

1. Although the cladistic analysis of the limb proportions of the Old World monkeys as well as of their environments points toward the conclusion that these primates experienced an ancestral terrestrial locomotor adaptation, the limb proportions of the New World primate Cebus are similar to those of the Old World monkeys. Further research is needed on the morphology of the limb bones of Cebus in comparison with not only the Old World monkeys but also with the remaining New World monkeys in order to establish the extent of the similarities and differences. This is important in answering the question of whether or not the post cranial proportions of the Old World monkeys arose as an adaptation to a terrestrial environment.

2. Further research is needed into the effect of a terrestrial quadrupedal locomotor pattern on the limb proportions of larger bodied primates. This is particularly important in view of the emerging evidence that many of the Miocene hominoids lived in woodland niches that would require at least a semiterrestrial locomotor pattern. In light of the evidence that the hominid line maintained the primitive limb proportions to a large body size, while the other hominoids experienced hindlimb reduction, it would be desirable to know the body size as well as specific locomotor circumstances resulting in hindlimb reduction. Such a study might includ not only further morphological analysis of fossil and extant primates, but also the static analysis of weight distribution, gait and energetics in larger bodied extant primates.
3. These allometric analyses have pointed toward the conclusion that the ancestral primate body proportions were consist nt with a below branch feeding adaptation. However, the analysis of the relationship between body weight and locomotor pattern has shown that locomotor specialisation appears to result at body weights over approximately 3000 grams. It would be desireable to analyise the morphology of the extant small bodied higher primates as well as the strepshrine primates in view of correlating differences in locomotor pattern with differences in postcranial morphology. The purpose would be to establish the degree to which the skeletons of these smaller bodied primates are specifically suited to particular locomotor adaptations. It would also be important to establish the degree to which body size increase effects the relationship between specific post cranial morphology and locomotor pattern.

These problems can be encompassed under the general need for further work into the energetics of locomotion, specific relationship between morphology and locomotion in the wild, and into the comparative ontogenetic patterns of primates of both similar and different postcranial proportions and locomotor patterns.

Appendix I. The Metrical Data for the Extant Higher Primates

Key to the abbreviations used in Appendix I

Collections

T.C. Smithsonian	Terry Collection, Smithsonian Institution, Washington D.C.
BM(NH)	British Museum (Natural History)
Powell Cotton	The Powell Cotton Collection, Birchington, Kent
Cam. Vet. Ana.	The collection of the Department of Vetinary Anatomy, Cambridge University
Cam. Zoo.	The collection of the Department of Zoology, Cambridge University
Cam. Duck.	The Duckworth Collection, Department of Anthropology, Cambridge University

Measurements

FESD	sagittal diameter of the midshaft of the femur
FETD	transverse diameter of the midshaft of the femur
FEAVD	average diameter of the midshaft of the femur
FECIR	circumference of the midshaft of the femur
FECT	average cortical thickness of the midshaft of the femur
FESCA	area of the cross section of the midshaft of the femur
FESECM	section modulus of the cross section of the midshaft of the femur - in the sagittal plane
FELENG	length of the femur
TILENG	length of the tibia
HLLENG	length of the hindlimb
HUSD	sagittal diameter of the midshaft of the humerus
HUTD	transverse diameter of the midshaft of the humerus
HUAVD	average diameter of the midshaft of the humerus
HUCIR	circumference of the midshaft of the humerus
HUCT	average cortical thickness of the midshaft of the humerus

HUSCA	area of the cross section of the midshaft of the humerus
HUSECM	section modulus of the cross section of the midshaft of the humerus - in the sagittal plane
HULENG	length of the humerus
RALENG	length of the radius
FLLENG	length of the forelimb
STLENG	skeletal trunk length
IMINDEX	intermembral index
BRINDEX	brachial index
CRURAL	crural index
FERINDEX	robusticity index of the femur
HURINDEX	robusticity index of the humerus

Statistics

N	number of skeletons of each sex of each species measured
MEAN	mean
STD. DEVIATION	standard deviation

HOMO SAPIENS -- NEGRO -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
T.C. SMITHSONIAN	581	32.80	30.35	30.58	93.00	9.41	626.18	2758.09	515.00	405.00	920.00
T.C. SMITHSONIAN	594	25.85	31.40	28.63	89.00	7.91	510.15	1978.47	489.00	401.00	890.00
T.C. SMITHSONIAN	595	28.35	27.90	27.13	87.00	7.88	501.30	2111.41	501.00	424.00	925.00
T.C. SMITHSONIAN	719	30.90	28.30	29.60	90.00	9.09	584.35	2596.05	425.00	376.00	801.00
T.C. SMITHSONIAN	821	31.05	26.65	28.85	89.00	6.90	475.31	2316.91	467.00	384.00	851.00
T.C. SMITHSONIAN	876	28.15	26.90	27.53	84.00	7.38	468.38	1977.98	486.00	398.00	886.00
T.C. SMITHSONIAN	885	33.85	31.65	32.75	101.00	7.11	575.29	3143.26	514.00	420.00	934.00
T.C. SMITHSONIAN	955	26.85	27.00	26.93	82.00	7.24	447.76	1817.47	441.00	364.00	807.00
T.C. SMITHSONIAN	987	34.25	28.10	31.18	96.00	7.06	529.71	2947.48	535.00	450.00	985.00
T.C. SMITHSONIAN	1013	35.40	26.55	30.98	97.00	8.46	587.29	3123.98	470.00	391.00	861.00
T.C. SMITHSONIAN	145	35.60	27.50	30.55	97.00	7.18	524.50	2786.21	521.00	427.00	948.00
T.C. SMITHSONIAN	565	31.40	27.90	29.65	91.00	7.89	540.74	2548.61	478.00	411.00	889.00
T.C. SMITHSONIAN	576	30.35	27.20	28.78	89.00	6.98	477.57	2271.68	446.00	367.00	813.00
T.C. SMITHSONIAN	792	30.90	26.65	28.78	88.00	6.83	469.92	2298.68	453.00	366.00	819.00
T.C. SMITHSONIAN	905	31.00	28.40	29.70	94.00	7.64	530.24	2573.74	502.00	423.00	925.00
T.C. SMITHSONIAN	1141	34.70	26.00	30.35	94.00	7.70	534.59	2905.93	517.00	439.00	956.00
T.C. SMITHSONIAN	13	27.95	24.50	26.23	83.00	5.15	344.05	1580.81	454.00	374.00	828.00
T.C. SMITHSONIAN	459	33.50	27.35	30.43	95.00	6.90	506.41	2730.68	507.00	402.00	909.00
T.C. SMITHSONIAN	881	29.40	27.85	28.63	89.00	7.19	484.23	2209.28	469.00	368.00	885.00
T.C. SMITHSONIAN	990	31.85	25.00	28.43	88.00	7.69	496.14	2368.70	435.00	342.00	777.00
	N	20	20	20	20	20	20	20	20	20	20
	MEAN	31.01	25.96	29.33	90.80	7.48	510.66	2452.22	481.35	396.30	880.35
	STD. DEVIATION	2.68	6.39	1.56	5.02	0.90	60.69	433.83	32.09	28.85	58.65

HOMO SAPIENS -- NEGRO -- FEMALE

COLLECTION	SPECIMEN NO.	FE3D	FE1D	FEAVD	FE1R	FECT	FE3A	FFSECM	FFLENG	TILENG	MLLENG
T.C. SMITHSONIAN	541	27.40	21.50	24.40	77.00	7.03	378.99	1519.06	417.00	340.00	757.00
T.C. SMITHSONIAN	632	28.10	27.25	27.68	82.00	6.30	422.99	1939.75	471.00	372.00	843.00
T.C. SMITHSONIAN	723	30.60	25.20	27.60	85.00	7.08	453.57	2095.17	447.00	364.00	831.00
T.C. SMITHSONIAN	913	27.90	24.50	26.20	80.00	5.89	378.05	1670.28	445.00	356.00	801.00
T.C. SMITHSONIAN	929	24.15	22.05	23.10	73.00	6.24	339.39	1200.93	436.00	359.00	795.00
T.C. SMITHSONIAN	996	29.55	25.30	27.43	86.00	6.45	423.30	1990.30	478.00	401.00	879.00
T.C. SMITHSONIAN	1076	27.85	20.70	24.28	78.00	4.61	290.44	1299.17	420.00	338.00	758.00
T.C. SMITHSONIAN	1215	26.15	27.10	26.63	84.00	6.16	396.22	1674.40	439.00	352.00	791.00
T.C. SMITHSONIAN	1315	29.55	26.70	28.28	88.00	6.14	427.58	2070.92	486.00	390.00	876.00
T.C. SMITHSONIAN	1413	25.90	25.55	25.73	80.00	5.79	362.64	1521.02	445.00	364.00	809.00
T.C. SMITHSONIAN	294	29.15	25.65	27.40	83.00	6.45	426.45	1963.99	460.00	373.00	833.00
T.C. SMITHSONIAN	729	28.90	22.65	25.78	82.00	7.05	411.87	1768.67	446.00	373.00	819.00
T.C. SMITHSONIAN	815	28.80	26.65	27.73	85.00	7.08	458.49	2042.02	458.00	374.00	832.00
T.C. SMITHSONIAN	1064	29.95	26.00	27.98	87.00	6.56	440.28	2097.34	441.00	326.00	767.00
T.C. SMITHSONIAN	1333	24.40	27.55	25.98	79.00	6.89	411.34	1512.40	411.00	350.00	761.00
T.C. SMITHSONIAN	1311	25.90	28.50	27.20	83.00	6.83	437.19	1722.12	415.00	338.00	753.00
T.C. SMITHSONIAN	255	27.20	27.70	27.45	84.00	6.49	427.45	1860.93	482.00	406.00	888.00
T.C. SMITHSONIAN	280	28.50	22.55	25.53	80.00	5.93	361.77	1639.65	431.00	356.00	787.00
T.C. SMITHSONIAN	568	26.00	24.05	25.03	78.00	5.83	352.44	1448.09	438.00	347.00	785.00
T.C. SMITHSONIAN	1402	22.80	24.70	23.75	75.00	7.21	374.15	1225.05	415.00	345.00	760.00
	N	20	20	20	20	20	20	20	20	20	20
	MEAN	27.47	25.09	26.26	81.45	6.40	398.28	1711.06	445.05	361.20	806.25
	STD. DEVIATION	2.08	2.24	1.53	4.02	0.67	43.75	289.87	23.44	21.14	42.84

HOMO SAPIENS -- CAUCASIAN -- MALE

COLLECTION	SPECIMEN NO.	FFSD	FFTD	FFAVD	FECIR	FECI	FECSA	FESECM	FFLENG	TILENG	HLLENG
T.C. SMITHSONIAN	131	29.30	28.05	28.68	87.00	7.28	488.97	2224.60	455.00	361.00	814.00
T.C. SMITHSONIAN	521	27.25	25.90	26.58	81.00	7.55	451.43	1916.73	463.00	372.00	835.00
T.C. SMITHSONIAN	755	30.75	28.75	29.75	92.00	7.14	507.17	2460.47	437.00	337.00	774.00
T.C. SMITHSONIAN	989	25.05	27.60	26.33	82.00	6.41	382.53	1543.22	448.00	351.00	799.00
T.C. SMITHSONIAN	1029	27.50	25.85	26.68	81.00	7.68	457.75	1956.10	465.00	372.01	837.10
T.C. SMITHSONIAN	1126	30.20	31.55	30.88	93.00	6.43	505.03	2478.43	491.00	389.00	879.00
T.C. SMITHSONIAN	1255	27.80	22.00	24.90	79.00	6.28	366.28	1553.04	437.00	352.00	789.00
T.C. SMITHSONIAN	111	26.20	25.00	25.60	78.00	5.40	357.61	1603.95	398.00	318.00	706.00
T.C. SMITHSONIAN	303	31.75	30.55	31.15	97.00	6.84	523.14	2494.84	492.00	406.00	898.00
T.C. SMITHSONIAN	641	28.20	27.70	27.95	88.00	7.58	485.33	2057.52	442.00	351.00	793.00
	N	10	10	10	10	10	10	10	10	10	10
	MEAN	28.40	27.30	27.85	86.00	6.68	444.51	1803.88	451.80	360.80	812.60
	STD. DEVIATION	2.09	2.77	2.20	6.45	1.06	75.61	711.51	29.97	25.17	54.65

HOMO SAPIENS -- CAUCASIAN -- FEMALE

COLLECTION	SPECIMEN NO.	FFSD	FETD	FFAVD	FECIR	FECI	FECSA	FESECM	FFLENG	TILENG	HLLENG
T.C. SMITHSONIAN	1153	24.40	26.50	25.45	79.00	5.91	362.18	1418.89	388.00	306.00	694.00
T.C. SMITHSONIAN	405	27.25	22.60	24.93	77.00	6.88	386.69	1579.70	392.00	303.00	695.00
T.C. SMITHSONIAN	880	26.60	25.00	25.80	78.00	6.58	396.66	1638.37	447.00	363.00	830.00
T.C. SMITHSONIAN	1523	26.80	26.05	26.43	81.00	4.83	339.41	1419.34	430.00	334.00	764.00
T.C. SMITHSONIAN	1563	27.65	23.50	25.58	79.00	5.74	355.49	1596.88	430.00	340.00	770.00
	N	5	5	5	5	5	5	5	5	5	5
	MEAN	26.54	24.73	25.60	78.80	5.99	368.11	1530.64	421.40	329.20	750.60
	STD. DEVIATION	1.24	1.66	0.55	1.48	0.80	23.32	104.01	32.43	25.03	57.35

GORILLA GORILLA -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1952.9.25.1	31.50	41.00	36.25	115.00	7.39	661.09	3534.72	347.00	271.00	617.00
BM(NH)	1949.12.30.2	30.20	41.15	35.68	116.00	8.50	708.17	3404.25	386.00	298.00	684.00
BM(NH)	1948.5.4.1	30.45	43.80	37.13	119.00	8.60	746.29	3660.52	378.00	305.00	683.00
BM(NH)	1963.2.27.1	31.00	37.05	34.03	106.00	7.33	609.06	3119.07	336.00	269.00	605.00
BM(NH)	1948.436	29.85	40.20	35.03	0.00	7.78	652.49	3193.91	385.00	292.00	677.00
BM(NH)	1961.4.5.1	34.15	43.70	38.93	121.00	9.86	890.61	4739.61	395.00	288.00	683.00
BM(NH)	1864.12.1.13	32.65	41.05	36.85	114.00	8.28	733.72	3907.09	382.00	300.00	682.00
BM(NH)	1948.3.3.2	33.90	39.55	36.73	114.00	8.20	733.18	4084.29	378.00	298.00	676.00
BM(NH)	1948.4.11	30.95	34.10	32.53	102.00	8.16	635.11	3051.22	361.00	277.00	638.00
	N	9	9	9	8	9	9	9	9	9	9
	MEAN	31.63	40.18	35.91	113.38	8.26	707.75	3632.74	371.78	288.56	660.33
	STD. DEVIATION	1.58	3.06	1.88	6.37	0.76	84.03	543.31	19.43	13.47	31.49

GORILLA GORILLA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1864.12.1.1	23.70	26.45	25.08	78.00	5.28	526.66	1278.61	288.00	218.00	506.00
BM(NH)	1864.12.1.5	23.90	29.05	26.48	83.00	5.15	542.88	1415.60	304.00	233.00	537.00
BM(NH)	1948.12.20.2	25.55	32.50	29.03	93.00	6.51	652.24	1868.63	318.00	254.00	572.00
BM(NH)	1976.439	27.30	31.90	29.60	93.00	5.96	639.70	2029.57	333.00	250.00	583.00
BM(NH)	1976.440	24.35	32.45	28.40	89.00	6.54	640.20	1731.21	303.00	238.00	541.00
BM(NH)	1916.11.11.1	24.05	30.25	27.15	86.00	7.38	654.78	1655.91	303.00	231.00	534.00
BM(NH)	1948.3.31.1	26.75	31.50	29.13	91.00	5.40	600.53	1878.48	317.00	252.00	569.00
	N	7	7	7	7	7	7	7	7	7	7
	MEAN	25.09	30.59	27.84	87.57	6.03	658.14	1694.00	309.43	239.43	548.86
	STD. DEVIATION	1.66	2.21	1.66	5.59	0.82	55.38	267.71	14.48	11.26	26.98

P&M TRIBOLOGISTS -- MALE

COLLECTIO	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FEPICM	FELENG	TILEJG	HLLENG
BM(AM)	1901.8.9.54	21.20	24.35	22.78	72.00	5.35	292.01	994.95	291.00	225.00	519.00
BM(AM)	1961.7.24.16	21.45	25.90	23.18	74.00	4.79	272.73	937.28	278.00	218.00	496.00
BM(NM)	1882.9.18.1	25.45	28.40	26.93	85.00	4.31	305.60	1425.10	298.00	224.00	522.00
BM(NM)	1924.8.6.1	21.45	25.00	23.23	73.00	6.69	345.30	1091.84	302.00	258.00	560.00
POWELL COTTON	491	0.00	0.00	0.00	70.00	0.00	0.00	0.00	302.00	245.00	547.00
POWELL COTTON	724	0.00	0.00	0.00	80.00	0.00	0.00	0.00	293.00	240.00	533.00
POWELL COTTON	998	0.00	0.00	0.00	74.00	0.00	0.00	0.00	301.00	236.00	537.00
POWELL COTTON	272	0.00	0.00	0.00	77.00	0.00	0.00	0.00	305.00	255.00	560.00
POWELL COTTON	256	0.00	0.00	0.00	75.00	0.00	0.00	0.00	302.00	245.00	547.00
POWELL COTTON	49	0.00	0.00	0.00	75.00	0.00	0.00	0.00	286.00	231.00	517.00
POWELL COTTON	25	0.00	0.00	0.00	83.00	0.00	0.00	0.00	314.00	255.00	569.00
POWELL COTTON	24	0.00	0.00	0.00	74.00	0.00	0.00	0.00	285.00	231.00	516.00
	N	4	4	4	12	4	4	4	12	12	12
	MEAN	22.14	25.91	24.03	76.00	5.29	303.91	1112.29	296.45	237.17	533.58
	STD. DEVIATION	2.25	1.78	1.94	4.69	1.03	30.71	218.07	10.09	12.02	20.69

PAN TROGLODYTES -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FFLENG	TILENG	HLLENG
BM(NH)	1851.7.27.8	21.90	23.20	22.50	74.00	4.31	247.51	948.30	291.00	228.00	519.00
BM(NH)	1948.5.7.2	16.70	15.60	16.15	52.00	2.96	122.52	365.07	240.00	200.00	440.00
BM(NH)	37.3356	20.30	23.90	22.10	71.00	4.64	252.95	859.86	280.00	217.00	477.00
BM(NH)	1946.6.27.1	24.60	25.50	25.05	78.00	5.03	316.35	1294.14	298.00	235.00	533.00
BM(NH)	37.3367	19.80	21.70	20.75	66.00	4.70	236.30	755.09	271.00	216.00	487.00
BM(NH)	1948.10.25.2	22.45	24.15	23.30	74.00	4.89	282.41	1061.04	305.00	249.00	554.00
BM(NH)	1976.437	7.10	4.03	23.72	9.88	5.62	880.02	7209.56	0.48	599.10	300.09
POWELL COTTON	967	0.00	0.00	0.00	75.00	0.00	0.00	0.00	272.00	215.00	487.00
POWELL COTTON	800	0.00	0.00	0.00	63.50	0.00	0.00	0.00	262.00	205.00	467.00
POWELL COTTON	664	0.00	0.00	0.00	64.00	0.00	0.00	0.00	301.00	237.00	538.00
POWELL COTTON	655	0.00	0.00	0.00	68.50	0.00	0.00	0.00	310.00	252.00	562.00
POWELL COTTON	650	0.00	0.00	0.00	70.50	0.00	0.00	0.00	291.00	241.00	532.00
POWELL COTTON	504	0.00	0.00	0.00	77.00	0.00	0.00	0.00	294.00	242.00	536.00
POWELL COTTON	501	0.00	0.00	0.00	74.00	0.00	0.00	0.00	285.00	227.00	512.00
POWELL COTTON	498	0.00	0.00	0.00	78.00	0.00	0.00	0.00	285.00	230.00	515.00
POWELL COTTON	467	0.00	0.00	0.00	76.00	0.00	0.00	0.00	304.00	235.00	539.00
POWELL COTTON	450	0.00	0.00	0.00	68.50	0.00	0.00	0.00	285.00	229.00	514.00
	N	7	7	7	17	7	7	7	17	17	17
	MEAN	21.39	22.71	22.05	70.94	4.04	247.26	918.74	285.71	229.41	515.12
	STD. DEVIATION	2.72	3.37	2.98	6.76	0.69	61.06	303.11	19.08	14.74	33.31

PUNGO PYGMAEUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	302	20.05	24.90	22.48	71.00	5.54	291.47	919.14	246.00	245.00	561.00
BM(NH)	1084	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	213.00	0.00
BM(NH)	1093	17.45	20.20	18.83	59.00	3.50	167.33	505.46	238.00	197.00	435.00
BM(NH)	1880.4.10.1	19.50	25.35	22.43	71.00	5.55	290.27	890.26	260.00	251.00	511.00
BM(NH)	1973.1570	21.70	25.60	23.15	73.00	6.40	332.51	1030.33	262.00	234.00	496.00
BM(NH)	31	17.70	21.00	19.35	62.00	3.99	202.10	610.21	270.00	227.00	497.00
BM(NH)	1968.10.25.1	19.60	23.40	21.50	68.00	6.34	300.13	860.10	281.00	234.00	515.00
BM(NH)	1080	21.15	26.80	23.98	71.00	5.91	332.22	1107.49	271.00	236.00	507.00
BM(NH)	1865.10.2.1	19.55	26.50	23.03	73.00	4.59	258.12	850.44	262.00	232.10	494.00
BM(NH)	1868.4.16.2	20.10	25.10	22.60	71.00	5.00	274.39	908.79	298.00	251.00	549.00
	N	9	9	9	9	9	9	9	9	10	9
	MEAN	19.53	24.32	21.93	68.78	5.20	272.06	853.60	273.78	232.00	507.89
	STD. DEVIATION	1.24	2.33	1.74	4.97	1.02	55.71	188.71	18.91	16.75	34.37

PUNGO PYGMAEUS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1880.4.10.2	14.70	18.85	16.78	55.00	4.63	174.34	385.28	230.00	194.00	424.00
BM(NH)	1948.7.6.1	15.30	19.45	17.38	55.00	4.10	168.52	412.04	239.00	201.00	440.00
BM(NH)	3P	0.00	0.00	0.00	48.00	0.00	0.00	0.00	228.00	190.00	418.00
CAM. SUCK.	51.0.5	0.00	0.00	0.00	56.00	0.00	0.00	0.00	237.00	197.00	434.00
	N	2	2	2	4	2	2	2	4	4	4
	MEAN	15.00	19.15	17.08	53.50	4.37	171.43	398.66	233.50	195.50	429.00
	STD. DEVIATION	0.42	0.42	0.42	3.70	0.37	4.12	18.97	5.32	4.65	9.87

MELANOTES MOLLERI -- MALE AND FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECN	FELENG	TILENG	HLLENG
CAM. VET. ANA.	M3	0.00	0.00	0.00	32.50	0.00	0.00	0.00	195.00	170.00	365.00
CAM. VET. B.M.	M1	0.00	0.00	0.00	31.00	0.00	0.00	0.00	214.40	182.40	396.80
CAM. VET. ANA.	M	0.00	0.00	0.00	32.00	0.00	0.00	0.00	197.90	170.00	367.90
CAM. VET. ANA.	M13	0.00	0.00	0.00	31.50	0.00	0.00	0.00	187.30	161.10	348.40
CAM. ZOO.	E71U0A	0.00	0.00	0.00	32.50	0.00	0.00	0.00	198.00	174.40	372.40
CAM. BUCK.	54.0.1	0.00	0.00	0.00	31.50	0.00	0.00	0.00	203.90	169.60	373.50
	N	0	0	0	6	0	0	0	6	6	6
	MEAN	0.00	0.00	0.00	31.83	0.00	0.00	0.00	199.12	171.28	370.23
	STD. DEVIATION	0.00	0.00	0.00	0.61	0.00	0.00	0.00	9.73	6.99	16.01

COLOBUS POLYKOMOS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECN	FELENG	TILENG	HLLENG
BM(NH)	1938.6.21.2	11.20	12.20	11.70	37.50	2.04	61.76	123.52	194.60	176.50	371.10
BM(NH)	72.158	11.95	12.85	12.40	38.50	2.30	72.87	151.69	189.60	175.80	365.40
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	11.58	12.53	12.05	38.00	2.17	67.32	137.61	192.10	176.15	368.25
	STD. DEVIATION	0.53	0.46	0.49	0.71	0.18	7.86	19.92	3.54	0.49	4.03

COLOBUS POLYKOMOS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECN	FELENG	TILENG	HLLENG
BM(NH)	1930.9.1.13	11.95	12.15	12.05	38.50	2.40	77.25	153.83	183.50	161.50	344.00
BM(NH)	11804	12.20	12.30	12.25	39.00	3.45	95.39	173.51	226.90	194.00	422.90
BM(NH)	1930.12.15.1	12.65	12.90	12.78	41.00	2.56	82.22	175.04	223.00	197.90	420.90
POWELL COTTON	98	0.00	0.00	0.00	42.50	0.00	0.00	0.00	207.20	189.10	396.30
	N	3	3	3	4	3	3	3	4	4	4
	MEAN	12.27	12.45	12.36	40.25	2.87	84.95	167.46	210.15	187.13	394.03
	STD. DEVIATION	0.39	0.40	0.38	1.85	0.50	9.17	11.83	19.17	19.84	36.73

COLOBUS BADIUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1930.8.1.2	11.45	11.95	11.70	38.00	2.70	76.36	141.58	174.10	154.70	332.90
BM(NH)	1931.8.1.1	12.05	11.80	11.93	38.00	2.31	69.98	142.23	195.30	170.60	365.90
BM(NH)	1963.108	10.65	11.60	11.13	36.50	2.66	70.64	119.46	173.90	150.10	324.00
BM(NH)	1963.7.25.1	10.70	10.80	10.75	34.50	2.89	71.36	116.29	187.30	160.00	347.30
BM(NH)	1966.6.5.1	10.25	11.00	10.63	34.50	2.09	55.93	98.17	184.40	159.80	344.20
BM(NH)	1901.8.9.46	11.50	12.40	11.95	38.50	2.65	77.28	145.09	180.60	154.20	334.80
BM(NH)	72.133	10.30	10.85	10.58	34.50	2.74	67.35	106.81	174.70	0.00	0.00
	N	7	7	7	7	7	7	7	7	6	6
	MEAN	10.99	11.49	11.24	36.36	2.58	69.84	124.23	182.04	156.23	341.50
	STD. DEVIATION	0.69	0.62	0.61	1.84	0.28	7.08	18.83	7.60	7.12	14.58

COLOBUS BADIUS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
CAM. DUCK.	40.109	10.35	11.30	10.83	35.00	2.40	63.46	107.89	183.40	159.50	342.90
CAM. DUCK.	778.13	10.95	10.95	10.95	35.50	2.46	65.66	116.98	185.70	155.70	341.40
CAM. DUCK.	1930.3.1.6	9.75	11.10	10.43	33.50	2.13	55.36	91.89	190.10	169.70	359.80
CAM. DUCK.	72.132	9.75	11.05	10.40	33.50	1.78	47.81	82.57	174.80	0.00	0.00
POWELL COTTON	215	0.00	0.00	0.00	37.50	0.00	0.00	0.00	187.40	162.00	349.40
	N	4	4	4	5	4	4	4	5	4	4
	MEAN	10.20	11.10	10.65	34.90	2.19	58.08	99.83	184.28	161.73	348.38
	STD. DEVIATION	0.57	0.15	0.28	1.64	0.31	8.15	15.49	9.84	5.91	8.17

COLORADO GUEREZA -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	72.149	11.00	11.25	11.13	36.00	1.85	53.98	106.70	179.00	160.30	339.90
BM(NH)	72.141	12.05	12.60	12.33	39.00	2.19	69.63	148.50	194.00	0.00	0.00
BM(NH)	72.139	12.85	14.00	13.43	43.00	2.53	86.38	0.00	205.00	0.00	0.00
BM(NH)	72.134	13.35	11.95	12.65	40.00	2.14	70.47	167.97	199.00	0.00	0.00
BM(NH)	72.151	12.15	12.15	12.15	38.50	2.75	81.24	161.24	199.30	0.00	0.00
BM(NH)	72.152	11.85	12.50	12.18	38.50	2.79	82.13	157.08	202.60	0.00	0.00
	N	6	6	6	6	6	6	5	6	1	1
	MEAN	12.21	12.41	12.31	39.17	2.38	73.97	148.24	196.48	160.30	339.90
	STD. DEVIATION	0.82	0.92	0.75	2.29	0.37	11.87	24.30	9.34	0.00	0.00

COLOBUS GUEREZA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	72.144	10.75	11.30	11.08	35.00	2.28	62.88	115.98	176.10	156.80	332.90
BM(NH)	72.150	10.20	10.45	10.58	34.00	2.15	57.31	0.00	172.50	0.00	0.00
BM(NH)	72.135	12.20	13.55	12.88	40.50	2.60	83.43	172.07	191.50	0.00	0.00
BM(NH)	72.140	13.00	13.75	13.38	43.00	2.48	84.70	192.57	210.50	0.00	0.00
BM(NH)	72.153	12.40	12.95	12.68	39.50	2.86	88.21	178.08	204.30	0.00	0.00
	N	5	5	5	5	5	5	4	5	1	1
	MEAN	11.83	12.40	12.12	38.40	2.47	75.35	164.45	190.94	156.80	332.90
	STD. DEVIATION	1.01	1.45	1.22	3.80	0.28	14.16	34.02	16.69	0.00	0.00

PSEUDOTIS OBSCURA -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	71.733	11.35	10.70	11.03	35.50	2.45	65.94	122.66	193.50	172.40	366.10
BM(NH)	71.709	10.00	10.70	10.35	34.00	2.46	60.94	94.96	171.60	149.10	320.50
BM(NH)	71.734	11.30	10.50	10.40	36.00	2.65	66.60	99.52	171.80	144.80	316.60
BM(NH)	71.722	10.55	10.75	10.65	34.00	2.74	68.04	110.73	192.00	163.60	355.60
BM(NH)	71.714	11.15	10.65	10.90	34.50	2.93	73.19	123.25	175.40	150.90	326.30
BM(NH)	71.728	10.05	11.15	10.60	34.50	2.68	62.96	100.78	182.00	150.70	332.70
BM(NH)	71.732	10.00	10.35	10.18	33.00	2.40	58.60	93.34	177.20	151.30	328.50
BM(NH)	71.735	10.40	10.65	10.63	34.00	2.49	62.10	103.55	176.60	151.90	330.50
BM(NH)	71.729	11.20	11.40	11.30	36.00	2.36	66.34	123.39	178.80	154.60	333.40
	N	9.	9	9	9	9	9	9	9	9	9
	MEAN	10.52	10.77	10.65	34.39	3.55	64.74	108.22	179.86	154.41	334.47
	STD. DEVIATION	0.57	0.33	0.36	0.89	0.19	4.16	12.08	8.01	8.45	16.14

PSEUDOTIS OBSCURA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	71.711	10.15	10.75	10.45	33.00	2.39	60.44	99.49	172.80	151.10	323.90
BM(NH)	71.707	9.65	10.00	9.83	31.50	2.43	56.58	84.75	175.70	150.90	326.60
BM(NH)	71.726	10.00	10.55	10.28	33.00	2.18	55.29	91.78	167.70	147.60	315.10
BM(NH)	71.708	9.15	10.15	9.65	32.00	2.09	49.46	74.75	159.10	137.10	296.60
BM(NH)	71.710	9.85	10.15	10.00	32.00	2.11	52.34	86.07	172.90	145.40	318 80
BM(NH)	71.720	10.60	10.90	10.75	34.00	2.69	68.17	111.63	165.00	143.20	308.20
BM(NH)	71.719	10.35	10.90	10.63	34.00	2.56	64.85	105.80	183.50	161.10	344.80
BM(NH)	71.751	10.90	11.35	11.13	35.50	2.21	61.94	115.32	182.40	159.80	342.20
BM(NH)	71.721	10.60	11.00	10.80	35.00	2.60	66.95	112.19	187.50	158.10	345.60
BM(NH)	71.737	10.10	10.40	10.25	33.00	2.28	56.99	94.25	168.70	147.70	316.40
BM(NH)	71.703	0.00	10.45	0.00	33.50	0.00	0.00	0.00	172.90	146.10	319.20
BM(NH)	71.736	10.60	10.90	10.75	34.50	2.16	58.34	105.07	165.50	144.00	309.50
BM(NH)	71.709	10.95	10.80	10.43	33.50	2.19	56.60	95.31	178.10	150.90	328.99
	N	12	13	12	13	12	12	12	13	13	13
	MEAN	10.17	10.64	10.41	33.42	2.32	58.98	98.05	173.23	149.49	322.76
	STD. DEVIATION	0.48	0.39	0.43	1.19	0.21	5.71	12.30	8.14	6.95	14.83

CERCOCEBUS TORQUATUS -- MALE

COLLECTION	SPECIMEN NO.	FESO	FETO	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1948.450	12.35	13.50	12.93	42.00	2.41	79.61	172.14	212.10	183.60	395.70
BM(NH)	1938.7.7.3	15.75	14.05	14.90	47.00	2.74	104.11	292.88	228.60	202.90	431.50
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	14.05	13.78	13.92	44.50	2.58	91.86	232.51	220.35	193.25	413.60
	STD. DEVIATION	2.40	0.39	1.39	3.54	0.23	17.32	85.38	11.67	13.65	25.31

CERCOCEBUS TORQUATUS -- FEMALE

COLLECTION	SPECIMEN NO.	FESO	FETO	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1859.2.8.2	9.95	10.70	10.33	33.50	1.70	46.48	84.73	141.40	142.20	303.60
BM(NH)	1939.12.6.1	10.50	10.70	10.60	34.50	1.74	48.37	91.89	179.00	159.60	338.60
BM(NH)	1938.7.7.4	12.10	11.25	11.68	37.00	2.08	62.44	135.86	171.70	156.10	327.80
BM(NH)	1939.7.7.5	12.05	11.85	11.95	38.00	1.73	55.41	127.40	178.30	159.90	338.00
	N	4	4	4	4	4	4	4	4	4	4
	MEAN	11.15	11.13	11.14	35.75	1.81	53.18	109.97	172.65	154.15	327.00
	STD. DEVIATION	1.09	0.59	0.79	2.10	0.18	7.27	25.42	8.21	8.26	16.37

CERCOCEBUS ALBIGENA -- MALE

COLLECTION	SPECIMEN NO.	FESO	FETO	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1930.8.1.25	11.20	10.20	10.70	34.00	2.01	54.95	105.49	199.50	175.00	374.50
BM(NH)	72.21	11.15	11.00	11.08	35.50	2.11	59.48	114.31	191.20	0.00	0.00
POWELL COTTON	683	0.00	0.00	0.00	39.50	0.00	0.00	0.00	214.80	196.30	411.10
POWELL COTTON	359	0.00	0.00	0.00	39.00	0.00	0.00	0.00	221.40	222.70	444.10
POWELL COTTON	768	0.00	0.00	0.00	41.00	0.00	0.00	0.00	219.30	191.10	410.40
POWELL COTTON	668	0.00	0.00	0.00	40.00	0.00	0.00	0.00	215.90	199.70	415.60
POWELL COTTON	971	0.00	0.00	0.00	39.00	0.00	0.00	0.00	210.70	190.50	401.20
POWELL COTTON	852	0.00	0.00	0.00	38.00	0.00	0.00	0.00	211.70	191.80	403.50
POWELL COTTON	769	0.00	0.00	0.00	40.00	0.00	0.00	0.00	211.80	191.50	403.30
	N	2	2	2	9	2	2	2	9	8	8
	MEAN	11.18	10.60	10.89	38.44	2.06	57.22	109.90	210.48	196.43	407.36
	STD. DEVIATION	0.04	0.57	0.27	2.28	0.07	3.20	6.24	9.40	13.36	18.47

CERCOCEBUS ALBIGENA -- FEMALE

COLLECTION	SPECIMEN NO.	FL3D	FETD	FEAVD	FECIR	FECI	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	72.22	10.00	9.70	9.85	32 00	1.94	48.17	81.98	174.00	0.00	0.00
POWELL COTTON	555	0.00	0.00	0.00	35 00	0.00	0.00	0.00	188.00	167.10	355.10
POWELL COTTON	807	0.00	0.00	0.00	34.50	0.00	0.00	0.00	190.60	170.80	361.40
POWELL COTTON	157	0.00	0.00	0.00	32.50	0.00	0.00	0.00	185.70	173.50	359.20
POWELL COTTON	716	0.00	0.00	0.00	32.50	0.00	0.00	0.00	183.60	164.10	347.90
POWELL COTTON	561	0.00	0.00	0.00	33.00	0.00	0.00	0.00	184.10	169.20	353.30
POWELL COTTON	721	0.00	0.00	0.00	35.00	0.00	0.00	0.00	186.60	173.00	359.60
POWELL COTTON	997	0.00	0.00	0.00	34.00	0.00	0.00	0.00	168.40	146.10	314.50
	N	1	1	1	8	1	1	1	8	7	7
	MEAN	10.00	9.70	9.85	33.56	1.94	48.17	81.98	182.63	166.57	350 43
	STD. DEVIATION	0.00	0.00	0.00	1.21	0.00	0.00	0.00	7.54	9.93	16.49

CERCOPITHECUS MITIS -- MALE

COLLECTION	SPECIMEN NO.	FL3D	FETD	FEAVD	FECIR	FECI	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	72.76	10.70	11.20	10.95	35.50	1.85	53.17	105.05	170.00	0.00	0.00
BM(NH)	72.68	11.45	11.20	11.33	36.50	2.08	60.31	122.54	177.50	0.00	0.00
BM(NH)	72.82	11.90	10.30	11.10	35.00	2.41	65.37	129.69	178.00	167.10	345.10
BM(NH)	72.86	9.35	10.35	9.85	32.00	1.79	45.39	75.76	164.00	159.50	323.50
BM(NH)	72.72	10.50	10.20	10.35	32.50	2.14	55.16	98.40	164.40	0.00	0.00
BM(NH)	72.60	10.85	11.20	11.03	36.00	2 40	65.07	117.05	172.60	0.00	0.00
BM(NH)	72.90	10.95	11.30	11.13	36.00	2.39	65.51	118.67	181 00	170.00	353.00
BM(NH)	72.65	10.95	10.40	10.68	34.00	2.09	56.27	106.91	171.90	161.80	333.70
BM(NH)	72.59	11.30	11.40	11.45	37.00	1.86	56.09	115.68	175.20	162.00	337.20
BM(NH)	72.53	10.65	11.50	11.08	34.00	1.69	45.75	99.01	173.80	0.00	0.00
BM(NH)	72.52	9.90	10.15	10.03	33.00	1.70	44.47	79.57	171.70	0.00	0.00
	N	11	11	11	11	11	11	11	11	5	5
	MEAN	10.77	10.85	10.82	34.86	2.04	55.49	104.19	172.92	164.04	338.46
	STD. DEVIATION	0.70	0.57	0.53	1.72	0.24	7.98	17.11	5.04	4.37	11.29

CERCOPITHECUS MITIS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
B4(NW)	72.90	9.05	9.05	9.05	29.00	1.55	36.52	59.60	146.00	135.20	281.20
B4(NW)	72.95	8.35	9.00	8.68	28.00	1.66	36.55	52.33	140.00	130.80	270.80
B4(NW)	72.78	10.15	9.90	10.03	31.00	1.63	42.88	79.00	148.10	0.00	0.00
B4(NW)	72.91	8.50	9.50	9.00	29.00	1.66	38.24	56.98	142.70	131.00	273.70
B4(NW)	72.97	8.50	8.55	8.53	27.00	1.83	38.41	54.06	141.20	136.10	277.30
B4(NW)	72.77	8.50	9.55	9.03	29.00	1.66	38.48	57.88	148.60	0.00	0.00
B4(NW)	72.81	9.05	9.65	9.35	30.00	1.38	34.48	59.19	141.50	133.80	275.30
B4(NW)	72.63	9.40	10.15	9.78	31.00	1.80	45.07	74.46	150.90	0.00	0.00
B4(NW)	72.66	9.00	9.45	9.23	29.50	1.90	43.68	65.79	142.70	135.00	277.70
B4(NW)	72.98	8.45	8.55	8.50	27.00	1.76	37.31	58.03	149.40	142.10	291.50
B4(NW)	72.62	8.20	8.55	8.38	27.50	1.53	32.83	47.81	133.80	127.80	261.60
B4(NW)	72.56	8.85	9.50	9.18	29.00	1.50	36.17	58.61	143.80	0.00	0.00
	N	12	12	12	12	12	12	12	12	8	8
	MEAN	8.83	9.28	9.06	29.08	0.16	638.59	60.30	144.06	133.98	276.14
	STD. DEVIATION	0.55	0.54	0.38	1.72	0.01	303.71	8.87	4.83	4.31	8.55

CERCOPITHECUS APTHIOPS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
B4(NW)	72.25	7.35	7.50	7.43	24.50	1.50	27.93	34.95	132.70	0.00	0.00
B4(NW)	72.32	7.10	7.90	7.50	24.50	1.46	27.65	33.63	129.80	0.00	0.00
B4(NW)	1930.A.1.15	8.35	7.90	8.13	25.50	1.51	31.38	46.12	127.80	119.80	247.60
B4(NW)	72.36	9.20	8.35	8.78	28.00	1.75	38.52	60.62	128.20	0.00	0.00
B4(NW)	72.27	8.95	9.35	9.15	29.50	1.78	41.14	63.70	137.00	0.00	0.00
B4(NW)	72.38	7.70	9.65	8.68	28.50	1.46	32.96	46.27	127.50	0.00	0.00
	N	6	6	6	6	6	6	6	6	1	1
	MEAN	8.11	8.46	8.28	26.83	1.58	33.26	47.52	129.83	119.80	247.60
	STD. DEVIATION	0.96	0.87	0.71	2.19	0.15	5.94	12.51	4.20	0.00	0.00

CERCOPITHECUS AETHIOPS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	72.33	9.30	9.50	9.40	30.00	1.81	43.34	70.64	151.50	0.00	0.00
BM(NH)	72.25	11.20	10.30	10.75	34.00	1.49	43.14	93.78	162.00	0.00	0.00
BM(NH)	72.29	9.35	8.15	8.75	28.00	1.86	40.16	62.13	144.60	0.00	0.00
BM(NH)	72.31	9.70	9.45	9.58	30.50	2.30	52.56	80.91	166.20	0.00	0.00
	N	4	4	4	4	4	4	4	4	0	0
	MEAN	9.99	9.35	9.62	30.63	1.87	44.80	76.87	156.08	0.00	0.00
	STD. DEVIATION	0.89	0.89	0.83	2.50	0.33	5.37	13.64	9.84	0.00	0.00

CERCOPITHECUS NEGLECTUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1972.47	10.75	10.45	10.60	34.00	2.45	62.72	109.26	170.10	161.10	331.20
BM(NH)	1972.50	11.10	11.20	11.15	36.00	2.06	59.02	116.53	147.70	157.90	325.60
POWELL COTTON	372	0.00	0.00	0.00	32.50	0.00	0.00	0.00	152.10	147.50	299.60
	N	2	2	2	3	2	2	2	3	3	3
	MEAN	10.93	10.83	10.88	34.17	2.26	60.87	112.90	163.30	155.50	318.80
	STD. DEVIATION	0.25	0.53	0.39	1.76	0.28	2.42	5.14	9.77	7.11	14.86

CERCOPITHECUS NEGLECTUS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1972.49	8.55	9.05	8.80	28.50	1.55	35.45	54.94	134.10	123.20	257.30
BM(NH)	1972.48	8.65	9.50	9.08	29.50	1.69	39.22	59.89	141.20	130.80	272.00
BM(NH)	1972.45	9.30	9.70	9.50	31.00	1.60	39.70	66.53	138.00	0.00	0.00
	N	3	3	3	3	3	3	3	3	2	2
	MEAN	8.83	9.42	9.15	29.67	1.61	38.12	60.45	137.77	127.00	264.65
	STD. DEVIATION	0.41	0.33	0.35	1.26	0.07	2.33	5.82	3.56	5.17	11.39

CERCOPITHECUS MONA -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1948.469	10.45	9.15	9.80	31.50	2.03	49.16	87.11	156.80	150.00	306.80
BM(NH)	1948.481	9.80	10.40	10.10	32.50	1.84	47.65	81.92	159.90	153.10	313.20
BM(NH)	1944.477	11.40	10.60	10.90	35.00	2.08	57.36	113.78	178.50	172.90	351.40
BM(NH)	1948.480	10.50	10.45	10.48	33.50	1.75	48.08	93.35	149.80	136.90	286.70
BM(NH)	1948.475	9.40	10.30	9.85	32.00	2.43	56.41	82.95	151.90	145.90	297.80
BM(NH)	1938.7.7.8	10.05	10.00	10.03	32.50	1.61	42.62	78.89	146.40	139.70	326.10
BM(NH)	1938.7.7.9	10.85	9.90	10.38	33.00	2.26	57 49	104.00	161.70	156.70	318.40
	N	7	7	7	7	7	7	7	7	7	7
	MEAN	10.35	10.09	10.22	32.86	2.00	51.25	91.71	160.71	153.59	314.34
	STD. DEVIATION	0.67	0.46	0.39	1.14	0.29	5.84	12.90	9 68	11.33	20.91

CERCOPITHECUS TALAPOIN -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1977.874	5.70	6.00	5.85	19.00	0.84	13.18	14.09	88.90	87.10	175.90
BM(NH)	1977.860	5.75	5.80	5.78	19.00	1.03	15.34	15.94	93.70	91.10	184.80
BM(NH)	1977.866	6.50	6.30	6.40	21.00	1.04	17.47	20.79	100.10	100.00	200.10
	N	3	3	3	3	3	3	3	3	3	3
	MEAN	5.98	6.03	6.01	19.67	0.97	15.33	16.94	94.23	92.70	186.93
	STD. DEVIATION	0.65	0.25	0.34	1.15	0.11	2.15	3.46	5.62	6.45	12.24

CERCOPITHECUS TALAPOIN -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1977.870	5.40	5.65	5.53	18.00	0.94	13.54	13.39	88.40	85.90	174.30
BM(NH)	1977.861	5.60	4.85	5.23	19.00	0.60	8 62	10.62	91.50	87.90	179.50
BM(NH)	1977.862	5.40	5.50	5.45	18.00	0.83	12.02	12.35	88.70	86.50	175.20
BM(NH)	1977.867	5.90	5.80	5.85	19.00	1.18	17.29	17.61	93.40	93.40	186.80
BM(NH)	1977.873	5.25	5.55	5.40	17.50	1.04	14.23	12.97	85.10	82.10	167.20
	N	5	5	5	5	5	5	5	5	5	5
	MEAN	5.51	5.47	5.49	18.30	0.92	13.14	13.39	89.42	87.16	176.58
	STD. DEVIATION	0.25	0.17	0.23	0.67	0.22	3.17	2.59	3.18	4.10	7.20

MACACA FASCICULARIS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1847.12.11.5	10.30	10.40	10.35	33.00	1.68	65.63	85.46	146.40	133.50	279.90

MACACA FASCICULARIS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1896.6.12.13	8.80	8.05	8.43	26.00	1.41	31.03	49.64	120.50	108.50	229.00
BM(NH)	1910.12.24.1	8.40	9.25	8.93	29.00	2.08	44.58	61.54	131.80	126.30	258.10
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	8.70	8.65	8.68	27.50	1.75	37.81	55.59	126.15	117.40	243.55
	STD. DEVIATION	0.14	0.85	0.35	2.12	0.47	9.58	8.41	7.99	12.59	20.58

MACACA FUSCATA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	90.8.15.2	10.35	11.15	10.75	34.50	1.85	51.84	97.46	146.40	132.80	279.20

MACACA MULATTA -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	398	11.70	10.75	11.23	36.00	2.55	69.32	132.17	163.00	152.00	315.00

MACACA NEMESTRINA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1933.11.9.1	10.75	10.95	10.85	34.00	2.33	62.30	110.85	151.90	139.90	287.80

MACACA SYLVANUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1936.4.5.1	13.90	15.00	14.45	45.50	3.33	116.04	260.39	201.50	176.60	378.10

MACACA SYLVANUS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1894.5.20.1	12.90	13.65	13.08	42.00	2.50	83.10	181.13	177.00	154.90	331.90

CERCOPITHECUS MITIS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1966.5.18.1	10.80	11.35	11.08	35.00	1.69	49.78	100.50	164.10	147.70	311.80

PAPIO ANUBIS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1935.2.14.1	18.85	19.40	19.13	60.00	4.63	210.62	627.45	246.50	210.00	456.50
BM(NH)	1948.8.3.2	16.10	16.75	16.43	54.00	4.14	159.64	399.02	236.60	203.00	439.60
BM(NH)	1862.6.26.1	14.55	17.15	15.85	52.00	3.54	135.64	320.76	247.00	205.90	452.90
	N	3	3	3	3	3	3	3	3	3	3
	MEAN	16.50	17.77	17.14	55.33	4.10	168.63	449.08	243.37	206.30	449.67
	STD. DEVIATION	2.18	1.63	1.75	4.16	0.55	38.27	159.37	5.87	3.42	8.90

PAPIO ANUBIS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1901.8.9.23	13.70	14.20	13.95	44.50	4.15	127.74	253.97	211.20	181.00	392.20
BM(NH)	1962.12.14.6	14.40	14.00	14.20	43.50	2.98	105.04	249.99	197.80	167.90	365.70
BM(NH)	1862.6.26.2	12.90	14.50	13.70	44.00	3.16	104.22	215.44	205.50	170.40	375.90
	N	3	3	3	3	3	3	3	3	3	3
	MEAN	13.67	14.23	13.95	44.67	3.43	112.33	239.80	204.83	173.10	377.93
	STD. DEVIATION	0.75	0.25	0.25	0.76	0.63	13.33	21.19	6.72	4.95	13.37

PAPIO URSINUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1973.1290	16.95	17.45	17.20	54.00	5.19	195.74	478.98	232.60	199.50	432.10

PAPIO CYNOCEPHALUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1942.7.6.13	17.20	16.50	16.85	54.00	3.95	160.43	436.51	254.20	214.90	469.10
BM(NH)	1972.129	16.15	16.30	16.23	52.50	3.40	137.00	370.68	280.00	244.10	524.10
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	16.68	16.40	16.54	53.25	3.68	148.72	403.60	267.10	229.50	496.60
	STD. DEVIATION	0.74	0.14	0.44	1.06	0.39	16.57	44.55	18.24	20.43	38.89

ALOUATTA PELZELNI -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1934.7.6.192	8.35	10.45	9.40	31.00	1.86	63.54	61.99	167.70	141.00	308.00

ALOUATTA SENICULUS -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1952.857	10.55	12.10	11.33	36.00	2.21	62.89	111.43	174.80	152.90	327.70

ALOUATTA SENICULUS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1931.10.16.1	8.90	10.40	9.65	31.50	2.04	48.76	73.13	152.00	129.70	277.70

ATELES PANISCUS -- SEX UNKNOWN

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	60.7.22.19	14.15	15.05	14.60	45.50	2.54	96.26	231.86	230.60	210.40	441.00

BRACHYTELES ARACHNOIDES -- SEX UNKNOWN

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1845.6.21.4	10.95	12.60	11.78	38.00	2.48	72.14	132.68	198.10	168.70	366.80

CEBUS ALBIFRONS -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	3.9.1.9	7.20	7.85	7.53	24.50	1.51	28.58	35.25	132.80	119.50	252.30

CEBUS APELLA -- MALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	3.9.1.4	8.90	9.00	8.95	28.50	2.13	45.56	64.69	145.00	129.80	274.80

CEBUS APELLA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	1948.10.20.2	7.35	7.40	7.38	24.00	1.21	23.49	31.71	123.80	110.70	234.50

LAGOTHRIX LAGOTRICHA -- FEMALE

COLLECTION	SPECIMEN NO.	FESD	FETD	FEAVD	FECIR	FECT	FECSA	FESECM	FELENG	TILENG	HLLENG
BM(NH)	72.1026	12.10	10.80	11.45	37.00	1.86	56.37	119.89	156.40	136.00	292.40

HOMO SAPIENS -- NEGRO -- MALE

COLLECTION	SPECIMEN NO.	HEAD	HEAD	HEAD	HEAD	HEAD	HEAD	HEAD	HEAD	HEAD	HEAD
T.C. SMITHSONIAN	581	23.25	17.70	21.48	65.00	4.38	265.99	858.72	353.00	279.00	632.00
T.C. SMITHSONIAN	594	24.10	23.70	23.90	72.00	5.71	326.58	1244.44	340.00	269.00	635.00
T.C. SMITHSONIAN	595	21.90	19.95	20.93	65.00	5.86	276.95	903.07	357.00	286.00	643.00
T.C. SMITHSONIAN	719	22.55	21.15	21.85	66.00	4.95	267.26	994.64	319.00	262.00	581.00
T.C. SMITHSONIAN	821	22.95	23.35	23.10	71.00	5.14	289.90	1085.35	327.00	253.00	580.00
T.C. SMITHSONIAN	826	23.15	19.75	21.45	65.00	6.49	303.94	1013.53	333.00	258.00	591.00
T.C. SMITHSONIAN	845	24.40	24.20	24.30	76.00	4.93	299.87	1230.56	349.00	283.00	632.00
T.C. SMITHSONIAN	955	20.40	19.70	20.05	63.00	5.54	252.43	771.71	315.00	251.00	566.00
T.C. SMITHSONIAN	987	22.75	25.35	24.05	76.00	3.08	210.92	1012.32	377.00	291.00	668.00
T.C. SMITHSONIAN	1013	25.55	24.15	24.85	76.00	4.99	311.74	1332.58	350.00	274.00	624.00
T.C. SMITHSONIAN	145	24.05	24.60	24.33	76.00	4.43	276.59	1166.58	385.00	284.00	669.00
T.C. SMITHSONIAN	565	25.75	24.85	25.30	76.00	5.29	332.33	1431.70	344.00	273.00	617.00
T.C. SMITHSONIAN	574	23.05	20.70	21.88	67.00	5.53	282.97	1015.04	324.00	249.00	573.00
T.C. SMITHSONIAN	792	25.50	25.90	25.70	79.00	4.19	283.12	1323.55	315.00	255.00	570.00
T.C. SMITHSONIAN	935	22.60	23.30	22.95	71.00	4.63	266.18	1011.97	362.00	268.00	630.00
T.C. SMITHSONIAN	1141	23.55	23.50	23.52	71.00	5.36	306.18	1158.89	362.00	290.00	652.00
T.C. SMITHSONIAN	13	20.35	19.50	19.93	62.00	4.16	206.14	698.68	322.00	243.00	585.00
T.C. SMITHSONIAN	859	21.75	24.00	22.88	71.00	4.63	264.35	969.90	355.00	248.00	623.00
T.C. SMITHSONIAN	881	24.75	24.05	24.40	75.00	5.86	342.15	1327.49	329.00	260.00	589.00
T.C. SMITHSONIAN	990	22.60	19.90	21.25	66.00	4.45	234.38	878.95	314.00	235.00	549.00
	N	20	20	20	20	20	20	20	20	20	20
	MEAN	23.25	22.56	22.91	70.45	4.98	279.90	1018.47	344.05	267.55	611.60
	STD. DEVIATION	1.52	2.22	1.72	5.23	0.77	36.63	201.66	22.35	15.14	36.20

HOMO SAPIENS -- NEGRO -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIP	HUCT	HUCSA	HUSECM	HULENC	SALENG	FLLENG
T.C. SMITHSONIAN	561	19.60	18.60	19.10	58.00	5.13	224.84	669.38	300.00	229.00	529.00
T.C. SMITHSONIAN	632	20.60	18.60	19.60	60.00	4.00	197.52	663.90	343.00	248.00	591.00
T.C. SMITHSONIAN	723	20.60	19.95	20.28	61.00	4.23	213.00	734.42	305.00	236.00	541.00
T.C. SMITHSONIAN	913	19.40	18.50	18.95	59.00	3.41	167.59	552.32	304.00	235.00	541.00
T.C. SMITHSONIAN	929	20.20	17.55	18.88	56.00	4.66	208.57	650.25	308.00	236.00	544.00
T.C. SMITHSONIAN	994	21.20	19.35	20.28	61.00	4.83	233.78	788.41	328.00	247.00	575.00
T.C. SMITHSONIAN	1074	20.55	19.20	19.88	59.00	3.46	178.68	645.13	302.00	223.00	525.00
T.C. SMITHSONIAN	1215	19.75	16.75	18.25	58.00	2.95	141.46	500.83	328.00	246.00	574.00
T.C. SMITHSONIAN	1315	18.80	18.15	18.48	58.00	4.11	185.53	574.95	322.00	252.00	574.00
T.C. SMITHSONIAN	1413	19.70	17.65	18.68	57.00	3.98	182.92	600.71	311.00	245.00	556.00
T.C. SMITHSONIAN	296	21.10	20.50	20.80	64.00	4.14	216.54	779.32	328.00	254.00	582.00
T.C. SMITHSONIAN	729	18.90	18.40	18.65	58.00	4.21	191.10	584.88	308.00	244.00	552.00
T.C. SMITHSONIAN	815	21.60	18.30	19.95	62.00	4.90	230.77	778.28	311.00	244.00	555.00
T.C. SMITHSONIAN	1064	21.10	20.20	20.65	65.00	3.68	198.66	696.63	291.00	219.00	510.00
T.C. SMITHSONIAN	1333	21.80	19.45	20.63	63.00	5.56	262.47	865.79	301.00	246.00	547.00
T.C. SMITHSONIAN	1311	19.45	20.00	19.73	62.00	3.80	190.41	645.81	291.00	230.00	521.00
T.C. SMITHSONIAN	255	23.40	18.90	21.15	66.00	3.03	174.88	717.49	344.00	273.00	617.00
T.C. SMITHSONIAN	280	20.15	18.30	19.23	60.00	3.24	163.07	576.69	303.00	225.00	526.00
T.C. SMITHSONIAN	569	18.60	19.65	19.13	59.00	3.63	176.41	569.06	295.00	234.00	529.00
T.C. SMITHSONIAN	1402	20.90	21.40	21.15	64.00	5.01	254.13	849.31	287.00	221.00	509.00
	N	20	20	20	20	20	20	20	20	20	20
	MEAN	18.57	18.97	19.67	60.50	4.10	199.62	672.15	288.30	241.75	534.85
	STD. DEVIATION	5.66	1.12	0.91	2.82	0.73	30.96	102.12	90.77	14.20	74.81

HOMO SAPIENS -- CAUCASIAN -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUFT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
T.C. SMITHSONIAN	131	22.35	19.95	21.15	67.00	4.76	244.53	887.49	327.00	247.00	574.00
T.C. SMITHSONIAN	591	23.60	22.33	22.95	66.00	5.19	311.74	1147.56	336.00	244.00	580.00
T.C. SMITHSONIAN	755	22.25	22.50	22.38	71.00	4.98	272.08	981.21	325.00	230.00	555.00
T.C. SMITHSONIAN	989	18.90	19.30	19.10	60.00	3.54	173.33	581.27	317.00	232.00	549.00
T.C. SMITHSONIAN	1023	19.30	19.80	19.55	63.00	5.60	245.40	700.52	336.00	252.00	588.00
T.C. SMITHSONIAN	1126	22.95	23.25	23.05	70.00	3.52	206.30	858.26	369.00	270.00	638.00
T.C. SMITHSONIAN	1255	20.90	21.50	21.20	64.00	4.44	233.92	902.64	320.00	234.00	554.00
T.C. SMITHSONIAN	111	18.55	17.95	18.25	57.00	4.69	199.96	578.16	294.00	207.00	501.00
T.C. SMITHSONIAN	303	24.10	20.55	22.33	67.00	4.30	242.51	998.56	340.00	264.00	613.00
T.C. SMITHSONIAN	641	20.30	20.40	20.35	62.00	6.04	271.65	800.05	317.00	236.00	553.00
	N	10	10	10	10	10	10	10	10	10	10
	MEAN	21.31	20.75	21.26	64.90	4.75	240.14	833.57	318.90	241.60	570.50
	STD. DEVIATION	2.00	1.63	1.66	4.48	0.90	40.07	182.51	30.94	19.15	37.83

HOMO SAPIENS -- CAUCASIAN -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUFT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
T.C. SMITHSONIAN	1153	17.65	19.85	18.75	59.00	4.10	188.98	554.29	299.00	205.00	504.00
T.C. SMITHSONIAN	405	20.05	19.40	19.73	60.00	3.16	164.97	588.99	264.00	194.00	458.00
T.C. SMITHSONIAN	880	21.00	18.10	19.55	62.00	2.91	153.64	571.06	319.00	234.00	553.00
T.C. SMITHSONIAN	1523	19.40	21.40	20.40	63.00	2.26	128.61	500.61	302.00	224.00	526.00
T.C. SMITHSONIAN	1563	17.40	19.35	18.38	57.00	3.94	178.08	513.73	307.00	224.00	531.00
	N	5	5	5	5	5	5	5	5	5	5
	MEAN	19.10	19.62	19.36	60.20	3.27	162.86	545.74	298.20	216.20	514.40
	STD. DEVIATION	1.55	1.19	0.80	2.39	0.76	23.33	37.57	20.58	16.25	36.02

GORILLA GORILLA -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1962.4.25.1	32.25	36.85	34.55	107.00	5.98	554.37	3083.88	406.00	334.00	743.00
BM(NH)	1947.12.10.2	35.20	36.35	35.78	108.00	7.30	629.13	3502.87	457.00	373.00	831.00
BM(NH)	1968.5.4.1	34.00	34.25	34.13	107.00	7.19	602.01	3429.64	466.00	370.00	836.00
BM(NH)	1948.2.27.1	33.15	34.70	33.93	104.00	6.16	537.00	3137.76	402.00	337.00	739.00
BM(NH)	1968.436	33.15	31.55	32.85	101.00	8.70	654.84	2967.89	440.00	348.00	788.00
BM(NH)	1961.4.5.1	36.35	42.70	39.53	117.00	6.98	714.82	4692.19	450.00	350.00	800.00
BM(NH)	1864.12.1.13	33.20	34.30	33.75	103.00	6.68	567.53	3199.53	442.00	365.00	807.00
BM(NH)	1968.3.3.2	32.45	34.95	33.70	104.00	5.98	523.24	3007.42	453.00	375.00	828.00
BM(NH)	1968.6.11	30.40	35.40	32.90	100.00	6.98	564.13	2843.55	431.00	346.00	777.00
	N	9	9	9	9	9	9	9	9	9	9
	MEAN	32.79	36.12	34.43	105.89	6.87	591.62	3319.30	439.56	355.33	794.22
	STD. DEVIATION	1.86	2.62	2.01	5.01	0.85	64.58	556.83	22.08	15.68	36.01

GORILLA GORILLA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1864.12.1.1	23.60	25.35	24.48	77.00	3.35	222.55	1018.59	346.00	289.00	635.00
BM(NH)	1864.12.1.5	25.35	24.55	24.95	78.00	3.80	252.38	1191.85	359.00	291.00	650.00
BM(NH)	1968.12.27.2	27.80	29.60	28.70	89.00	4.43	337.27	1738.95	383.00	293.00	676.00
BM(NH)	1976.439	25.00	26.30	25.65	81.00	5.04	325.96	1390.82	388.00	303.00	691.00
BM(NH)	1976.440	24.35	27.55	25.95	81.00	5.06	330.45	1369.18	364.00	305.00	667.00
BM(NH)	1916.11.11.1	27.50	26.50	27.00	84.00	4.79	335.17	1590.66	337.00	278.00	615.00
BM(NH)	1949.3.31.1	24.40	25.60	25.00	78.00	4.44	287.20	1258.73	373.00	305.00	678.00
	N	7	7	7	7	7	7	7	7	7	7
	MEAN	25.43	26.49	25.94	81.14	4.42	298.38	1365.51	364.29	294.57	659.86
	STD. DEVIATION	1.62	1.67	1.46	4.22	0.64	48.08	242.43	18.69	9.76	26.87

PAN TROGLODYTES -- MALE

COLLECTION	SPECIMEN ID.	HUMD	HUTD	HUAVD	HUCIR	HJCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1901.8.9.P4	22.20	19.75	20.98	65.00	4.14	219.22	815.51	292.00	267.00	559.00
BM(NH)	1861.7.29.14	23.20	20.65	21.93	70.00	3.99	224.76	901.53	276.10	255.10	531.00
BM(NH)	1582.9.18.1	28.70	25.05	26.88	82.00	4.19	297.73	1558.54	531.00	276.00	577.00
BM(NH)	1924.8.6.1	21.80	22.60	22.20	68.00	5.04	271.54	961.51	314.00	281.00	599.00
POWELL COTTON	401	0.00	0.00	0.00	64.00	0.00	0.00	0.00	321.00	290.00	611.00
POWELL COTTON	724	0.00	0.00	0.00	81.00	0.00	0.00	0.00	293.00	281.00	574.00
POWELL COTTON	938	0.00	0.00	0.00	70.00	0.00	0.00	0.00	303.00	281.00	584.00
POWELL COTTON	272	0.00	0.00	0.00	72.00	0.00	0.00	0.00	306.00	284.00	590.00
POWELL COTTON	254	0.00	0.00	0.00	69.00	0.00	0.00	0.00	297.00	259.00	556.00
POWELL COTTON	49	0.00	0.00	0.00	74.00	0.00	0.00	0.00	290.00	271.00	561.00
POWELL COTTON	25	0.00	0.00	0.00	82.00	0.00	0.00	0.00	318.00	299.00	617.00
POWELL COTTON	24	0.00	0.00	0.00	67.00	0.00	0.00	0.00	284.00	266.00	550.00
	N	4	4	4	12	4	4	4	12	12	12
	MEAN	23.98	22.01	23.00	72.00	4.34	253.31	1059.17	275.17	275.83	575.75
	STD. DEVIATION	3.20	2.35	2.64	6.44	0.47	37.78	338.13	87.79	12.79	25.79

PAN TROGLODYTES -- FEMALE

COLLECTION	SPECIMEN NO.	HUFD	HUTD	HUAVD	HJCIR	HUCI	HUCSA	HUSFCH	HULENG	RALENG	FLLENG
BM(NH)	1851.7.27.A	24.85	21.70	23.28	74.00	4.00	241.55	1064.84	296.00	269.00	565.00
BM(H)	1949.5.7.2	14.85	15.70	17.28	55.00	3.16	138.05	463.26	240.00	217.00	457.00
BM(NH)	57.3564	21.30	19.00	20.40	64.00	3.70	194.35	728.59	285.00	270.00	555.00
BM(NH)	1968.5.27.1	23.90	22.20	23.00	73.00	4.68	271.32	1053 28	297.00	287.00	584.00
BM(NH)	57.5547	20.40	17.50	18.80	61.00	3.99	185.22	613.26	275.00	256.00	531.00
BM(NH)	1948.10.25.2	23.90	22.70	23.35	71.00	5.20	296.35	1154.56	293.00	300.00	593.00
BM(NH)	1976.457	40.08	0.02	50.02	240.52	4.95	245.00	7600.43	27.27	911.47	473.03
POWELL COTTON	267	0.00	0.00	0.00	74.50	0.00	0.00	0.00	277.00	260.00	537.00
POWELL COTTON	830	0.00	0.00	0.00	61.00	0.00	0.00	0.00	262.00	237.00	499.00
POWELL COTTON	664	0.00	0.00	0.00	59 00	0.00	0.00	0.00	315.00	288.00	603.00
POWELL COTTON	455	0.00	0.00	0.00	66.00	0.00	0.00	0.00	327.00	290.00	617.00
POWELL COTTON	659	0.00	0.00	0.00	65.50	0.00	0.00	0.00	299.00	284.00	583.00
POWELL COTTON	504	0.00	0.00	0.00	71.50	0.00	0.00	0.00	305.00	285.00	590.00
POWELL COTTON	501	0.00	0.00	0.00	71.00	0.00	0.00	0.00	304.00	265.00	569.00
POWELL COTTON	498	0.00	0.00	0.00	73.00	0.00	0.00	0.00	310.00	270.00	580.00
POWELL COTTON	467	0.00	0.00	0.00	73.00	0.00	0.00	0.00	294.00	269.00	563.00
POWELL COTTON	450	0.00	0.00	0.00	70.50	0.00	0.00	0.00	294.00	269.00	563.00
	N	7	7	7	17	7	7	7	17	17	17
	MEAN	22.39	20.15	21.27	67.76	3.44	223.52	866.91	291.82	269.98	561.71
	STD. DEVIATION	2.22	2.77	2.47	5.93	1.64	54.19	264.26	20.42	20.25	39.04

PONGO PYGMAEUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(M)	102	27.30	23.75	25.28	78.00	5.50	340.67	1517.31	381.00	396.00	777.00
BM(M)	1084	24.55	21.70	23.13	72.00	5.43	301.04	1176.71	348.00	331.00	679.00
BM(MM)	1093	22.15	19.00	20.58	64.00	3.13	170.85	693.04	316.00	304.00	620.00
BM(MM)	1580.4.10.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	373.00	0.00
BM(MM)	1973.1570	26.95	27.45	27.20	85.00	4.99	348.05	1626.39	330.00	341.00	671.00
BM(MM)	31	24.05	20.10	22.08	69.00	2.23	138.75	660.35	352.00	352.00	704.00
BM(MM)	1948.10.25.1	26.65	22.30	24.48	76.00	5.28	317.53	1377.93	351.00	371.00	721.00
BM(M)	1080	26.95	24.65	25.80	80.00	5.50	351.37	1548.98	353.00	364.00	717.00
BM(MM)	1845.10.2.1	26.45	23.00	24.83	78.00	4.78	300.63	1357.20	357.00	357.00	714.00
BM(MM)	1868.4.16.2	29.20	26.85	28.03	86.00	4.41	327.67	1726.73	378.00	404.00	782.00
	N	9	9	9	9	9	9	9	9	10	9
	MEAN	26.05	23.14	27.60	76.44	4.58	288.51	1299.29	351.78	359.20	697.22
	STD. DEVIATION	2.10	2.95	9.73	7.18	1.16	78.40	387.28	20.43	29.67	92.34

PONGO PYGMAEUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1880.4.10.2	21.20	19.85	20.53	63.00	4.06	210.03	755.80	293.00	303.00	596.00
BM(NH)	1948.7.6.1	19.95	19.10	19.53	60.00	4.13	199.54	661.50	312.00	318.00	630.00
BM(NH)	1P	0.00	0.00	0.00	53.00	0.00	0.00	0.00	295.00	304.00	599.00
CAM. DUCK.	51.0.5	0.00	0.00	0.00	63.00	0.00	0.00	0.00	299.00	299.00	598.00
	N	2	2	2	4	2	2	2	4	4	4
	MEAN	20.58	19.48	20.03	59.75	4.10	204.79	708.65	299.75	306.00	605.75
	STD. DEVIATION	0.88	0.53	0.71	4.72	0.05	7.42	66.68	8.54	8.29	14.71

HELOBATES MULLERI -- MALE AND FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
CAM. VET. ANA.	13	0.00	0.00	0.00	31.00	0.00	0.00	0.00	229.10	266.60	495.70
CAM. VET. ANA.	M1	0.00	0.00	0.00	30.50	0.00	0.00	0.00	246.50	277.40	523.90
CAM. VET. ANA.	M	0.00	0.00	0.00	30.50	0.00	0.00	0.00	232.30	263.90	496.20
CAM. VET. ANA.	M13	0.00	0.00	0.00	29.50	0.00	0.00	0.00	220.30	245.70	466.00
CAM. ZOO.	C7100A	0.00	0.00	0.00	33.00	0.00	0.00	0.00	237.10	270.50	507.60
CAM. DUCK.	54.0.1	0.00	0.00	0.00	30.00	0.00	0.00	0.00	226.40	267.50	493.90
	N	0	0	0	6	0	0	0	6	6	6
	MEAN	0.00	0.00	0.00	30.75	0.00	0.00	0.00	231.95	625.27	497.22
	STD. DEVIATION	0.00	0.00	0.00	1.21	0.00	0.00	0.00	9.09	10.44	19.02

COLOBUS POLYKOMOS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1930.8.1.13	11.20	10.50	10.85	34.00	2.04	56.34	109.89	145.90	140.10	286.00
BM(NH)	1180A	11.00	10.75	10.88	35.00	2.76	70.59	119.04	163.20	163.00	326.20
BM(NH)	1930.12.15.1	11.50	10.70	11.10	35.50	2.10	59.32	117.89	165.20	163.90	329.10
PURFLL COTTON	98	0.00	0.00	0.00	38.00	0.00	0.00	0.00	162.30	162.90	325.20
	N	3	3	3	4	3	3	3	4	4	4
	MEAN	11.23	10.65	10.94	35.63	2.30	62.08	115.61	158.65	157.53	316.13
	STD. DEVIATION	0.25	0.13	0.14	1.70	0.40	7.52	4.98	9.91	11.62	21.48

COLOBUS POLYKOMOS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1936.6.21.2	8.75	10.25	9.50	30.50	1.83	43.95	67.01	153.90	149.50	303.40
BM(NH)	72.158	10.35	10.20	10.28	32.50	1.88	49.56	91.79	146.60	149.40	296.00
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	9.55	10.23	9.89	31.50	1.86	46.76	79.40	150.15	149.95	299.10
	STD. DEVIATION	1.13	0.04	0.55	1.41	0.04	4.97	17.52	5.10	1.78	6.08

COLOBUS BADIUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1930.8.1.2	11.15	11.40	11.28	36.00	2.48	68.41	124.94	151.40	144.20	295.60
BM(NH)	1930.8.1.1	10.70	12.15	11.43	34.00	1.93	57.57	112.86	154.80	159.00	313.80
BM(NH)	1940.108	11.30	11.80	11.55	35.50	2.46	70.27	131.62	146.10	146.10	292.20
BM(NH)	1968.7.25.1	9.40	10.30	9.85	31.00	2.35	53.66	76.28	150.40	144.70	297.10
BM(NH)	1936.6.5.1	9.05	9.40	9.23	30.00	1.81	42.18	64.92	141.20	139.70	281.90
BM(NH)	1901.8.9.46	10.45	10.25	10.35	34.00	2.14	55.18	96.15	154.90	145.80	300.70
BM(NH)	72.133	9.65	10.20	9.93	32.00	2.24	53.98	84.11	148.00	0.00	0.00
	N	7	7	7	7	7	7	7	7	6	6
	MEAN	10.19	10.79	9.06	33.50	2.20	57.32	98.73	149.54	146.92	296.72
	STD. DEVIATION	0.98	1.00	3.53	2.50	0.26	9.57	25.33	4.91	6.46	10.77

COLOBUS BADIUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
CAM. DUCK.	40.109	10.25	11.55	10.90	34.50	2.14	58.87	104.40	153.30	152.60	305.90
CAM. DUCK.	778.13	10.55	10.75	10.65	33.00	2.10	56.40	101.36	151.50	146.10	297.60
CAM. DUCK.	1930.3.1.6	9.50	8.80	9.15	30.00	1.99	44.71	69.63	155.30	149.70	305.00
CAM. DUCK.	72.132	9.15	9.00	9.08	29.50	1.29	31.50	55.12	137.50	0.00	0.00
POWELL COTTON	215	0.00	0.00	0.00	36.50	0.00	0.00	0.00	156.70	157.60	314.30
	N	4	4	4	5	4	4	4	5	4	4
	MEAN	9.86	10.03	9.95	27.75	1.88	47.87	82.63	150.50	151.50	305.20
	STD. DEVIATION	0.65	1.34	0.96	12.41	0.40	12.54	24.16	7.50	4.80	6.97

COLOBUS GUEREZA -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUID	HUAVD	HUCIR	HUCT	HULSA	HUSECM	HULLNG	RALLNG	FLLLNG
BM(NH)	72.147	9.50	9.15	9.23	29.00	1.76	41.52	66.36	139.20	135.20	274.40
BM(NH)	72.141	11.10	10.75	10.93	35.00	1.83	52.21	103.39	151.70	0.00	0.00
BM(NH)	72.139	11.65	11.65	11.65	37.00	2.36	68.96	134.87	154.80	0.00	0.00
BM(NH)	72.134	10.75	10.15	10.45	33.00	1.96	57.34	96.96	155.80	0.00	0.00
BM(NH)	72.151	10.55	10.40	10.48	33.00	2.34	59.80	102.21	159.80	0.00	0.00
BM(NH)	72.152	10.50	11.15	10.83	34.50	2.39	63.23	108.99	156.00	0.00	0.00
	N	6	6	6	6	6	6	6	6	1	1
	MEAN	10.64	10.54	10.60	33.58	2.11	56.25	102.13	152.88	135.20	274.40
	STD. DEVIATION	0.78	0.87	0.80	2.69	0.29	9.68	22.03	7.19	0.00	0.00

COLOBUS GUEREZA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUID	HUAVD	HUCIR	HUCT	HULSA	HUSECM	HULLNG	RALLNG	FLLLNG
BM(NH)	72.148	9.30	8.50	8.90	28.00	2.00	43.39	64.98	142.50	134.70	277.20
BM(NH)	72.150	8.80	8.70	8.75	27.50	1.61	36.16	55.84	132.80	0.00	0.00
BM(NH)	72.138	10.95	10.90	10.93	34.50	2.01	56.36	107.40	149.50	0.00	0.00
BM(NH)	72.140	11.40	10.85	11.13	35.00	2.00	57.28	115.77	160.20	0.00	0.00
BM(NH)	72.153	9.95	9.80	9.88	31.00	2.25	53.90	86.79	152.80	0.00	0.00
	N	5	5	5	5	5	5	5	5	1	1
	MEAN	10.08	9.75	9.92	31.20	1.97	59.42	86.16	147.68	134.70	277.20
	STD. DEVIATION	1.09	1.14	1.11	3.51	0.23	9.25	25.96	10.61	0.00	0.00

PEROMYSCUS OBSCURUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSLCN	HULENG	RALENG	FLLENG
BM(NH)	71,715	9,90	9,45	9,68	31,00	2,12	51,88	82,48	156,50	148,70	305,00
BM(NH)	71,709	9,20	8,25	8,73	27,50	2,00	42,12	62,73	137,70	137,60	275,30
BM(NH)	71,734	8,20	8,75	8,78	28,50	2,23	45 81	62,10	133,10	129,90	261,00
BM(H)	71,722	9,60	9,45	9,53	30,50	2,15	49,89	74,94	147 50	141,10	288,60
BM(H)	71,710	9,15	9,05	9,10	29,50	2,40	50,52	70,90	135,50	136,90	272,40
BM(H)	71,728	10,30	10,05	10,18	32,00	2,02	51,60	90,60	138,80	138,70	277,50
BM(NH)	71,732	9,40	9,15	9,28	29,50	2,09	47,28	71,07	141,00	133,60	274,60
BM(NH)	71,735	8,90	9,35	9,13	29,50	2,05	45,53	65,61	139,80	136,50	276,40
BM(NH)	71,729	9,75	10,30	10,03	22,00	1,81	46,72	80,03	141,70	136,50	278,20
	N	9	9	9	9	9	9	9	9	9	9
	MEAN	9,44	9,32	9,38	28 89	2,10	47,93	73,64	141,16	137,72	278,82
	STD. DEVIATION	0,49	0,63	0,51	2,90	0,16	3,27	9,67	6,98	5,18	11,48

PEROMYSCUS OBSCURUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSLCN	HULENG	RALENG	FLLENG
BM(NH)	71,711	8,30	7,75	8,03	26,00	1,76	34,63	47,24	139,00	135 60	274,60
BM(NH)	71,737	8,30	8,15	8,23	27,00	1,83	36,69	49,88	142,60	140,20	282,80
BM(NH)	71,724	9,30	8,50	8,90	28,50	1,50	34,84	57,87	136,30	131,50	267 80
BM(H)	71,708	8,95	8,95	8 95	29,00	1,69	38,51	59,31	130,10	128,50	258 60
BM(NH)	71,710	9,40	8,55	8,98	29,00	1,94	35,79	61,08	134,70	132,10	266 80
BM(NH)	71,720	9,15	9,70	9,43	30,00	2,05	47,46	71,67	132,40	133,20	265,60
BM(NH)	71,719	9,90	9,25	9,58	30,50	1,86	45,14	76,01	150 40	146,80	297,20
BM(NH)	71,751	9,55	10,00	9,78	31,50	1,59	40,86	71,80	144,00	144,50	288,50
BM(NH)	71,721	10,10	9,60	9,85	31,50	2,03	49,93	83,26	145,00	142,70	287,70
BM(NH)	71,737	8,90	9,15	9,03	28,50	1,85	41,71	62,87	139,90	135,50	275,40
BM(NH)	71,703	9,05	9,55	9,30	30,00	1,79	42,18	66,05	139,00	135,20	274,20
BM(H)	71,736	9,20	9,80	9,50	30,50	1,65	40,62	65,67	130,60	127,60	258,20
BM(NH)	71,709	8,85	8,80	8,83	28,50	1,79	39,52	59,23	136,90	135,60	272,50
	N	13	13	13	13	13	13	13	13	13	13
	MEAN	9,15	9,06	9,11	29,27	1,76	40,60	64,00	138,48	136,06	274,59
	STD. DEVIATION	0,53	0,68	0,55	1,63	0,17	4,74	10,06	5,92	5,96	11,77

CERCOCEBUS TORQUATUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1948.650	11.80	13.25	12.53	38.50	2.78	84.73	163.83	166.90	171.80	338.70
BM(NH)	1938.7.7.3	12.85	14.55	13.70	42.00	2 71	93.32	205.00	180.90	189.20	370.10
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	12.33	13.90	13 12	40.25	2.75	89 03	184 42	171.90	180.50	354.40
	STD. DEVIATION	0.74	0 92	0.83	2.47	0.05	6.07	29.11	9.90	12.30	22 20

CERCOCEBUS TORQUATUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1859.2 8.2	8.15	9.45	8.80	27 50	1.93	41.48	55.98	127.80	133.80	260.60
BM(NH)	1935.12.6.1	9.30	10.30	9.80	30.50	1.84	45.95	74.89	143.10	147.10	290.20
BM(NH)	1938.7.7.4	9.40	11.10	10.45	32.00	1.88	50.51	88.35	137.20	141.20	278.40
BM(NH)	1938.7.7.5	9.25	11.35	10.30	32.00	1.49	40.85	71.59	146.00	148.40	294.40
	N	4	4	4	4	4	4	4	4	4	4
	MEAN	9.13	10.55	9.84	30.50	1.79	44.70	72.70	138.53	141.88	280.40
	STD. DEVIATION	0.70	0 86	0 75	2.12	0.20	4 49	13.30	8.03	8.02	16.03

CERCOCEBUS ALBIGENA -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1930.8.1.25	9.45	10.10	9.78	31 00	2.06	49.91	78 52	157.00	149.00	306.00
BM(NH)	72.21	9.80	10.70	10 25	31.50	1.96	50.96	85.74	142.00	0.00	0.00
POWELL COTTON	689	0.00	0.00	0.00	35 00	0.00	0.00	0.00	166.90	170.60	337.50
POWELL COTTON	339	0.00	0.00	0 00	34.00	0.00	0.00	0.00	179.20	174.00	353.20
POWELL COTTON	748	0.00	0.00	0.00	38.00	0.00	0.00	0.00	163.40	164.30	327.70
POWELL COTTON	668	0.00	0.00	0 00	34 00	0.00	0 00	0.00	165.10	169.10	334.20
POWELL COTTON	371	0.00	0.00	0.00	36.00	0.00	0.00	0.00	167.70	163.70	331.40
POWELL COTTON	852	0.00	0.00	0.00	34.00	0.00	0.00	0.00	162.20	164.80	327.00
POWELL COTTON	749	0.00	0.00	0.00	35.00	0.00	0.00	0.00	170.80	160.40	331 20
	N	8	8	8	9	8	8	8	9	8	8
	MEAN	9.63	10.40	10.02	34.28	0 20	150.44	82.13	163.81	164.49	331.05
	STD. DEVIATION	0.25	0.42	0.33	2.14	0.14	200.76	5.11	10.23	7.42	13.08

CERCOCEBUS ALBIGENA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	72.22	8.10	9.50	8.80	28.00	1.65	36.87	52.10	135.90	0.00	0.00
POWELL COTTON	355	0.00	0.00	0.00	30.50	0.00	0.00	0.00	147.10	143.10	290.20
POWELL COTTON	807	0.00	0.00	0.00	31.90	0.00	0.00	0.00	151.90	143.50	300.60
POWELL COTTON	157	0.00	0.00	0.00	29.50	0.00	0.00	0.00	145.00	149.60	294.60
POWELL COTTON	7 A	0.00	0.00	0.00	29.70	0.00	0.00	0.00	144.70	141.40	286.10
POWELL COTTON	561	0.00	0.00	0.00	29.00	0.00	0.00	0.00	142.60	142.10	284.70
POWELL COTTON	721	0.00	0.00	0.00	31.50	0.00	0.00	0.00	147.90	148.10	296.00
POWELL COTTON	797	0.00	0.00	0.00	31.00	0.00	0.00	0.00	130.30	130.10	260.40
	N	1	1	1	8	1	1	1	8	7	7
	MEAN	8.10	9.50	8.80	29.94	1.65	36.87	52.10	143.18	143.27	287.49
	STD. DEVIATION	0.00	0.00	0.00	1.24	0.00	0.00	0.00	6.95	6.70	13.17

CERCOPITHECUS MITIS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	72.76	9.05	11.50	10.28	33.00	2.24	55.82	83.52	145.80	0.00	0.00
BM(NH)	72.68	9.55	11.70	10.63	34.50	2.15	57.01	93.02	147.70	0.00	0.00
BM(NH)	72.82	9.05	11.35	10.05	35.00	2.34	56.07	81.55	143.70	139.90	283.60
BM(NH)	72.88	8.10	10.70	9.40	30.50	1.83	42.74	59.73	137.50	132.50	270.00
BM(NH)	72.72	8.00	9.40	8.70	28.00	2.26	45.51	56.09	138.90	0.00	0.00
BM(NH)	72.60	9.45	11.50	10.48	34.00	2.33	59.18	91.99	147.60	0.00	0.00
BM(NH)	72.90	9.50	10.50	10.00	32.00	2.49	58.59	87.03	141.90	142.10	284.00
BM(NH)	72.65	9.10	10.20	10.65	35.00	2.19	57.35	89.52	145.00	139.80	284.80
BM(NH)	72.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	133.60	0.00
BM(NH)	72.53	8.80	10.80	9.80	31.00	1.73	41.41	69.02	139.80	0.00	0.00
BM(NH)	72.52	7.55	10.00	9.78	29.00	1.78	38.39	49.26	139.70	0.00	0.00
		10	10	10	10	10	10	10	10	5	6
	MEA										

CEBUS APELLA MITIS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	72.91	6.65	8.40	7.65	25.00	1.64	30.78	35.89	120.70	114.80	235.50
BM(NH)	72.85	7.70	8.75	8.25	26.50	1.66	34.26	45.07	115.60	109.70	225.30
BM(NH)	72.79	7.50	9.50	8.65	28.00	1.46	32.97	46.60	120.10	0.00	0.00
BM(NH)	72.83	7.50	9.05	8.28	26.50	1.74	35.72	45.29	118.50	107.40	225.90
BM(NH)	72.87	7.05	9.15	8.10	26.50	1.78	33.65	40.29	120.90	117.00	237.90
BM(NH)	72.77	7.40	9.05	8.23	27.00	1.65	33.91	42.95	123.40	0.00	0.00
BM(NH)	72.31	7.25	9.30	8.28	27.00	1.66	34.42	42.88	115.20	111.70	229.90
BM(NH)	72.63	7.50	10.30	8.90	28.50	1.84	40.14	50.98	126.50	0.00	0.00
BM(NH)	72.46	7.30	9.85	8.58	27.50	1.99	40.36	47.55	122.60	116.50	239.10
BM(NH)	72.58	7.20	8.35	7.78	24.50	1.86	34.53	39.72	124.00	118.10	242.10
BM(NH)	72.62	7.05	8.85	7.95	25.50	1.74	33.95	39.82	112.60	107.70	220.30
BM(NH)	72.54	6.65	8.25	7.45	24.00	1.41	26.65	31.90	119.00	0.00	0.00
	N	12	12	12	12	12	12	12	12	6	8
	MEAN	7.25	9.08	8.16	26.38	1.70	34.19	42.17	120.19	112.86	232.03
	STD. DEVIATION	0.36	0.60	0.43	1.38	0.16	3.85	5.67	3.77	4.50	7.75

CEBUS APELLA APELLA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	72.23	7.10	7.00	7.05	23.00	1.93	31.00	33.10	101.00	0.00	0.00
BM(NH)	72.57	6.45	7.95	7.10	23.50	1.51	26.16	27.15	109.20	0.00	0.00
BM(NH)	1930.8.1.15	6.95	9.15	8.00	26.00	1.50	30.54	36.96	110.80	109.40	219.20
BM(NH)	72.36	7.40	9.80	8.60	27.00	1.93	39.87	48.41	112.50	0.00	0.00
BM(NH)	72.27	8.90	9.65	9.28	28.50	1.83	42.63	44.69	114.40	0.00	0.00
BM(NH)	72.50	7.20	9.20	8.20	24.00	1.89	37.25	43.59	110.30	0.00	0.00
	N	6	6	6	6	6	6	6	6	1	1
	MEAN	7.28	8.76	8.03	25.67	1.60	34.56	42.32	109.65	108.40	219.20
	STD. DEVIATION	0.69	1.09	0.86	2.09	0.43	6.32	15.29	4.63	0.00	0.00

CERCOPITHECUS ALTIOPS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	72.55	7.50	9.95	8.63	27.50	1.58	34.59	44.95	128.70	295.50	0.00
BM(NH)	72.65	9.05	10.25	9.65	30.50	1.51	38.49	63.88	134.50	0.00	0.00
BM(NH)	72.29	7.80	9.45	8.63	27.00	2.10	42.60	52.32	124.30	295.70	0.00
BM(NH)	72.31	8.60	10.40	9.50	30.00	2.20	50.06	69.44	137.60	318.00	0.00
	N	4	4	4	4	4	4	4	4	0	0
	MEAN	8.19	10.01	9.10	28.75	1.85	41.41	57.65	124.35	0.00	0.00
	STD. DEVIATION	0.79	0.42	0.55	1.76	0.35	6.62	11.07	16.57	0.00	0.00

CERCOPITHECUS NEGLECTUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1972.47	8.70	11.30	10.00	33.00	2.34	55.30	77.16	141.20	132.70	273.90
BM(NH)	1972.50	9.50	11.85	10.68	35.00	2.40	62.49	97.62	141.10	130.80	271.90
POWELL COTTON	372	0.00	0.00	0.00	31.00	0.00	0.00	0.00	132.00	128.20	260.20
	N	2	2	2	3	2	2	2	3	3	3
	MEAN	9.10	11.58	10.34	33.00	2.37	58.90	87.39	138.10	130.57	268.67
	STD. DEVIATION	0.57	0.39	0.48	2.00	0.04	5.08	14.47	5.28	2.26	7.40

CERCOPITHECUS NEGLECTUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1972.49	7.95	8.95	8.45	26.50	1.59	34.34	48.21	117.90	104.50	224.40
BM(NH)	1972.48	7.50	9.45	8.48	27.00	1.85	38.84	48.55	120.10	109.90	229.00
BM(NH)	1972.45	8.30	10.75	9.53	30.00	1.76	43.34	64.19	119.90	0.00	0.00
	N	3	3	3	3	3	3	3	3	2	2
	MEAN	7.92	9.72	8.82	27.83	1.73	38.84	53.65	119.30	107.20	226.70
	STD. DEVIATION	0.40	0.93	0.62	1.89	0.13	4.50	9.31	1.22	1.70	3.25

CERCOPITHECUS AETHIOPS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCBA	HUSECM	HULENG	BALENG	FLLENG
B4(NH)	1968.469	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	124.00	0.00
B4(NH)	1968.481	7.75	10.55	9.15	30.00	2.26	48.41	59.09	130.10	127.00	257.00
B4(NH)	1968.479	9.15	13.75	11.45	36.50	2.74	71.77	104.33	149.20	152.80	302.00
B4(NH)	1968.480	8.30	10.05	9.18	29.50	1.89	47.94	60.30	124.80	119.30	244.10
B4(NH)	1968.475	8.85	9.50	9.13	29.00	2.08	46.21	66.33	126.50	129.50	256.00
B4(NH)	1938.7.7.8	8.95	10.20	9.58	30.00	1.78	43.50	68.71	135.60	134.00	269.60
B4(NH)	1939.7.7.9	8.45	10.00	9.23	30.00	2.11	44.93	64.24	118.50	124.60	242.10
	N	6	6	6	6	6	6	6	6	7	6
	MEAN	8.58	10.68	9.63	30.83	2.14	49.96	70.51	136.08	130.63	265.25
	STD. DEVIATION	0.51	1.54	0.91	2.80	0.34	10.88	16.96	9.05	10.49	19.82

CERCOPITHECUS TALAPOIN -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCBA	HUSECM	HULENG	BALENG	FLLENG
B4(NH)	1977.874	4.90	5.05	4.98	16.50	0.86	11.15	9.81	75.30	74.10	149.40
B4(NH)	1977.868	4.80	6.10	5.45	17.50	1.15	15.15	12.31	77.20	80.50	157.70
B4(NH)	1977.866	5.10	6.20	5.65	18.00	0.98	14.15	12.81	84.90	87.40	172.30
	N	3	3	3	3	3	3	3	3	3	3
	MEAN	4.93	5.78	5.36	17.33	0.99	13.48	11.64	79.13	76.67	159.80
	STD. DEVIATION	0.15	0.64	0.34	0.76	0.14	2.08	1.61	5.08	3.91	11.59

CERCOPITHECUS TALAPOIN -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCBA	HUSECM	HULENG	BALENG	FLLENG
B4(NH)	1977.870	4.65	5.40	5.03	16.00	0.93	12.02	10.01	75.10	76.00	151.10
B4(NH)	1977.861	5.05	5.30	5.18	16.50	0.74	10.30	10.02	77.20	76.20	153.40
B4(NH)	1977.862	4.80	5.15	4.98	16.00	0.83	10.76	9.41	74.50	73.50	148.00
B4(NH)	1977.867	5.35	6.05	5.70	18.00	0.96	14.25	13.62	79.00	81.40	160.40
B4(NH)	1977.873	4.80	5.20	5.00	16.00	0.99	12.48	10.34	73.40	72.30	145.70
	N	5	5	5	5	5	5	5	5	5	5
	MEAN	4.93	5.42	4.58	16.50	0.89	11.96	10.68	75.84	75.88	151.72
	STD. DEVIATION	0.28	0.37	1.37	0.87	0.10	1.56	1.68	2.24	3.50	5.67

MACACA FASCICULARIS -- ALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1867.12.11.5	8.15	10.95	9.55	30.00	7.25	50.39	65.56	130 90	133.50	264.40

MACACA FASCICULARIS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1874.6.12.13	6.35	8.30	7.33	23.00	1.25	23.64	27.27	114.00	108.90	222.90
BM(NH)	1910.12.24.1	8.10	9.15	8.75	27.50	1.84	39.78	55.55	121.50	122 40	244.10
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	7.33	8.73	8.03	25.25	1.55	31.71	41.41	118.75	115.75	234.50
	STD. DEVIATION	1.18	0.60	0.99	3.18	0.42	11.41	20.00	6.72	9.69	16.40

MACACA FUSCATA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	50.8.15.2	9.75	10.95	10.35	32.50	1.89	50.01	85.52	131.50	135.10	266.60

MACACA MULATTA -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	30G	10.05	11.65	10.75	34.00	2.91	69.86	107.78	141.20	143.00	284.20

MACACA NEMESTRINA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1933.11.9.1	9.75	11.65	10.70	34.00	2.43	63.04	100.67	138.10	143.60	281.70

MACACA SILVANUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1859.4.9.1	12.50	13.70	14.00	43.00	3.49	112.99	219.55	167.20	175.10	342.30

MACACA SYLVANUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1834.3.20.1	12.40	13.25	12.83	38.00	2.04	89.23	140.98	149.40	150.00	299.40

CYNOPITHECUS NIGER -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1966.5.18.1	8.90	11.75	10.33	32.50	1.80	47.44	73.54	144.50	148.00	292 50

PAPIO ANUBIS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALE G	FLLE G
BM(NH)	1935.2.14.1	17.00	17.95	17.48	56 00	4.75	189.82	484.12	224.00	236 50	460.50
BM(NH)	1948.8.3.2	16.50	16.55	16.53	50.50	3.95	156.07	408.09	211.50	226.10	437.40
BM(NH)	1862.6.26.1	15.60	13.80	14.70	46.50	3.19	115.18	293.55	224.40	244.00	468.40
	N	3	3	3	3	3	3	3	3	3	3
	MEAN	16.37	16.10	16.24	51.00	3.96	153.69	396.59	219.90	235.47	455.37
	STD. DEVIATION	0.71	2.11	1.41	4.77	0.78	37.38	97.79	7.45	8.98	16.08

PAPIO ANUBIS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1901.8.9.23	12.65	14.30	13.47	42.00	3.83	115.54	216.87	196.10	208.90	405.00
BM(NH)	1962.12.14.6	13.10	14.20	13.65	42.00	2.95	99.00	214.29	180 00	185.70	365.70
BM(NH)	1862.6.26.2	12.70	12.70	12.70	40.00	2 55	81.41	177.68	185.90	196.40	382.30
	N	3	3	3	3	3	3	3	3	3	3
	MEAN	12.82	13.73	13.27	41.33	3.11	98.65	202.95	187.33	196.10	384.67
	STD. DEVIATION	0.25	0 90	0 50	1.15	0.65	17.07	21.92	8.15	10.60	18.69

PAPIO URSINUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1973.1290	16.19	17.20	16.68	52.00	4.96	182.45	428.93	202.00	213.40	415.40

PAPIO CYNOCEPHALUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1962.7.6.13	15.40	16.65	16.03	50.00	3.13	126.70	337.46	227.00	234.50	461.50
BM(NH)	1972.129	16.00	17.20	16.60	51.00	3.31	138.14	376.70	244.10	272.80	516.90
	N	2	2	2	2	2	2	2	2	2	2
	MEAN	15.70	16.93	16.32	50 50	3 22	132.42	357.08	235.56	254.45	490.20
	STD. DEVIATION	3.96	0.39	0.40	0.71	0.13	8.09	27.75	17.09	25.47	37.76

ALOUATTA BELZEBUL -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1904.7.6.192	9.40	9.70	9.55	30.50	1.79	43.57	70.95	155.30	143.10	298.40

ALOUATTA SENICULUS -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1932.857	11.50	12.00	11.75	36.50	2.00	61.28	122.43	171.20	151.40	322.60

ALOUATTA SENICULUS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1931.10.16.1	8.00	9.50	8.65	28.00	1.80	38.41	50.77	146.50	127.20	273.70

ATELES PANISCUS -- SEX UNKNOWN

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	60.7.22.19	11.90	11.55	11.73	37.00	2.26	67.23	138.40	233.30	227.10	461.00

BRACHYTELES ARACHNOIDES -- SEX UNKNOWN

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1845.6.21.6	11.55	10.20	10.88	34.00	2.28	61.29	117.95	200.50	191.90	392.40

CEBUS ALBIFRONS -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	5.9.1.5	6.80	7.20	7.00	22.50	1.40	24.63	28.62	105.30	99.20	204.50

CEBUS APELLA -- MALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	5.9.1.4	8.80	9.45	9.13	29.00	2.45	51.30	68.16	118.20	113.30	231.50

CEBUS APELLA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	1948.10.20.2	7.00	7.30	7.15	23.00	1.18	22.09	26.90	104.00	94.50	198.50

LAGOTHRIX LAGOTHRICHA -- FEMALE

COLLECTION	SPECIMEN NO.	HUSD	HUTD	HUAVD	HUCIR	HUCT	HUCSA	HUSECM	HULENG	RALENG	FLLENG
BM(NH)	72.1026	10.90	10.75	10.83	34.00	1.93	53.83	103.31	153.50	131.00	284.50

HOMO SAPIENS -- NEGRO -- MALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	EPIINDEX	CRINDEX	FEMINDEX	HUMINDEX
T.C. SMITHSONIAN	581	552.20	69.00	79.00	79.00	18.00	18.00
T.C. SMITHSONIAN	594	522.20	71.00	74.00	82.00	18.00	20.00
T.C. SMITHSONIAN	595	536.60	70.00	80.00	85.00	17.00	18.00
T.C. SMITHSONIAN	719	494.90	73.00	82.00	89.00	21.00	21.00
T.C. SMITHSONIAN	821	497.99	68.00	77.00	82.00	19.00	22.00
T.C. SMITHSONIAN	876	514.90	67.00	78.00	82.00	17.00	20.00
T.C. SMITHSONIAN	885	557.99	70.00	77.00	82.00	20.00	21.00
T.C. SMITHSONIAN	955	493.30	70.00	80.00	82.00	19.00	20.00
T.C. SMITHSONIAN	987	561.30	68.00	77.00	84.00	18.00	20.00
T.C. SMITHSONIAN	1013	502.99	73.00	78.00	83.00	21.00	22.00
T.C. SMITHSONIAN	145	579.50	69.00	74.00	82.00	19.00	20.00
T.C. SMITHSONIAN	565	518.70	71.00	79.00	86.00	19.00	22.00
T.C. SMITHSONIAN	574	498.20	70.00	77.00	82.00	20.00	21.00
T.C. SMITHSONIAN	792	530.40	68.00	81.00	81.00	19.00	25.00
T.C. SMITHSONIAN	905	571.50	68.00	74.00	84.00	19.00	20.00
T.C. SMITHSONIAN	1141	583.90	71.00	80.00	85.00	18.00	20.00
T.C. SMITHSONIAN	13	537.30	71.00	82.00	82.00	18.00	19.00
T.C. SMITHSONIAN	859	564.90	69.00	76.00	79.00	19.00	20.00
T.C. SMITHSONIAN	881	533.70	67.00	79.00	78.00	19.00	23.00
T.C. SMITHSONIAN	990	479.80	71.00	75.00	79.00	20.00	21.00
	N	20	20	20	20	20	20
	MEAN	531.96	69.65	77.90	82.40	18.90	20.65
	STD. DEVIATION	31.25	1.73	2.47	2.64	1.12	1.63

HOMO SAPIE .. -- NEGRO -- FEMALE

COLLECTIO.	SPECIMEN NO.	SILE IG	IMINDEX	ORBINDEX	CRINDEX	FEMINDEX	TUBINDEX
T.C. SMITHSONIAN	561	475.00	70.00	76.00	82.00	19.00	19.00
T.C. SMITHSONIAN	632	511.80	70.00	72.00	79.00	17.00	18.00
T.C. SMITHSONIAN	773	475.70	65.00	77.00	78.00	18.00	20.00
T.C. SMITHSONIAN	913	468.20	68.00	77.00	80.00	18.00	19.00
T.C. SMITHSONIAN	924	505.40	68.00	77.00	82.00	17.00	18.00
T.C. SMITHSONIAN	994	517.10	65.00	75.00	84.00	18.00	19.00
T.C. SMITHSONIAN	1076	488.40	69.00	74.00	81.00	19.00	20.00
T.C. SMITHSONIAN	1215	498.10	73.00	75.00	80.00	19.00	19.00
T.C. SMITHSONIAN	1315	512.60	66.00	78.00	80.00	18.00	18.00
T.C. SMITHSONIAN	1413	545.90	69.00	79.00	82.00	18.00	18.00
T.C. SMITHSONIAN	294	504.40	70.00	77.00	81.00	18.00	20.00
T.C. SMITHSONIAN	729	511.20	67.00	79.00	84.00	18.00	19.00
T.C. SMITHSONIAN	815	514.70	67.00	79.00	82.00	19.00	20.00
T.C. SMITHSONIAN	1064	504.50	67.00	75.00	74.00	20.00	22.00
T.C. SMITHSONIAN	1333	482.99	72.00	92.00	85.00	19.00	21.00
T.C. SMITHSONIAN	1311	493.30	69.00	79.00	82.00	20.00	21.00
T.C. SMITHSONIAN	255	515.80	70.00	79.00	84.00	17.00	19.00
T.C. SMITHSONIAN	280	472.40	69.00	74.00	83.00	19.00	20.00
T.C. SMITHSONIAN	568	465.99	67.00	79.00	82.00	19.00	20.00
T.C. SMITHSONIAN	1402	490.70	67.00	77.00	79.00	17.00	22.00
	N	20	20	20	20	20	20
	MEAN	497.71	68.40	77.00	81.25	18.35	19.55
	STD. DEVIATIO	20.46	2.11	2.36	2.55	0.88	1.28

HOMO SAPIENS -- CAUCASIAN -- MALE

COLLECTION	SPECIMEN NO.	STLENG	INDEX	BRINDEX	CRIINDEX	FERINDEX	HUPINDEX
T.C. SMITHSONIAN	131	505.80	70.00	76.00	79.00	19.00	21.00
T.C. SMITHSONIAN	591	526.50	70.00	73.00	80.00	18.00	20.00
T.C. SMITHSONIAN	755	530.60	72.00	71.00	77.00	21.00	22.00
T.C. SMITHSONIAN	989	525.70	69.00	73.00	78.00	18.00	19.00
T.C. SMITHSONIAN	1023	538.80	70.00	75.00	80.00	18.00	19.00
T.C. SMITHSONIAN	1126	573.90	73.00	73.00	79.00	19.00	19.00
T.C. SMITHSONIAN	1255	463.60	70.00	73.00	81.00	18.00	20.00
T.C. SMITHSONIAN	111	507.30	71.00	70.00	82.00	20.00	19.00
T.C. SMITHSONIAN	303	541.20	68.00	76.00	83.00	20.00	19.00
T.C. SMITHSONIAN	641	473.20	70.00	74.00	79.00	20.00	20.00
	N	10	10	10	10	10	10
	MEAN	518.66	70.30	73.40	79.80	19.10	19.80
	STD. DEVIATION	32.68	1.42	1.96	1.81	1.10	1.03

HOMO SAPIENS -- CAUCASIAN -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	INDEX	BRINDEX	CRIINDEX	FERINDEX	HUPINDEX
T.C. SMITHSONIAN	1153	512.10	73.00	69.00	79.00	20.00	20.00
T.C. SMITHSONIAN	405	521.40	66.00	74.00	77.00	20.00	23.00
T.C. SMITHSONIAN	880	537.10	67.00	73.00	78.00	17.00	19.00
T.C. SMITHSONIAN	1523	556.00	69.00	74.00	78.00	19.00	21.00
T.C. SMITHSONIAN	1563	524.40	69.00	73.00	79.00	18.00	19.00
	N	5	5	5	5	5	5
	MEAN	530.20	68.80	72.60	78.20	18.90	20.40
	STD. DEVIATION	16.97	2.68	2.07	0.84	1.30	1.67

GORILLA GORILLA -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	MURINDEX
BM(NH)	1862.5.25.1	599.15	120.00	82.00	78.00	33.00	26.00
BM(NH)	1949.12.30.2	647.25	121.00	82.00	77.00	30.00	24.00
BM(NH)	1949 5.4.1	664.20	122.00	79.00	81.00	32.00	23.00
BM(NH)	1949.2.27.1	579.70	122.00	84.00	80.00	32.00	26.00
BM(NH)	1948.436	640.40	116.00	79.00	76.00	0.00	23.00
BM(NH)	1961.4.5.1	741.60	118.00	78.00	73.00	31.00	26.00
BM(NH)	1864.12 1.13	615.00	118.00	83.00	79.00	30.00	23.00
BM(NH)	1948.3 3.2	652.20	123.00	83.00	79.00	30.00	23.00
BM(NH)	1945.4.11	0.00	122.00	80.00	77.00	28.00	23.00
	N	8	9	9	9	8	9
	MEAN	642.44	120.22	81.11	77.78	30.75	24.11
	STD. DEV ATION	49.27	2.39	2.15	2.39	1.58	1.45

GORILLA GORILLA -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	MURINDEX
BM(NH)	1864.12.1.1	530.12	126.00	84.00	76.00	27.00	22.00
BM(NH)	1864.12.1.5	477.85	121.00	81.00	77.00	27.00	22.00
BM(NH)	1949 12.20.2	571.80	118.00	77.00	80.00	29.00	23.00
BM(NH)	1976.439	592.95	119.00	78.00	75.00	28.00	21.00
BM(NH)	1976.440	542.70	123.00	83.00	79.00	29.00	22.00
BM(NH)	1916.11.11.1	502.55	115.00	83.00	76.00	28.00	25.00
BM(NH)	1948.3.31.1	539.90	119.00	82.00	80.00	29.00	21.00
	N	7	7	7	7	7	7
	MEAN	536.30	120.14	81.14	77.57	29.14	22.29
	STD. DEVIATION	35.90	3.58	2.67	2.07	0.90	1.38

PAN T-USE BYTES -- HALF

COLLECTIO	SPECIMEN NO.	SILE S	I4INDEX	BRINDEX	CRI DEX	FERI DEX	HURINDEX
B4(HH)	19[illegible].9.24	45[illegible].25	108.00	91.00	78.00	25.00	22.00
B4(HH)	1961.7.27.14	458.20	107.00	92.00	78.00	27.00	25.00
B4(HH)	1982 V.15.1	466.25	110.00	92.00	75.00	29.00	27.00
B4(HH)	1924.3.6 1	467.50	107.00	88.00	85.00	24.00	21.00
POWELL COTTOI	401	0.00	112.00	90.00	81.00	23.00	20.00
POWELL COTTOI	724	0.00	108.00	96.00	82.00	27.00	28.00
POWELL COTTOI	988	0.00	109.00	93.00	78.00	25.00	23.00
POWELL COTTO	272	0.00	109.00	93.00	77.00	25.00	24.00
POWELL COTTOI	254	0.00	102.00	87.00	81.00	25.00	23.00
POWELL COTTOI	49	0.00	109.00	93.00	81.00	26.00	26.00
POWELL COTTOI	25	0.00	105.00	94.00	81.00	26.00	26.00
POWELL COTTOI	24	0.00	107.00	94.00	81.00	26.00	24.00
	N	*	12	12	12	12	12
	MEAI	462.63	108.00	91.92	79.83	25.67	24.08
	STD. DEVIATION	5.12	2.37	2.57	2.69	1.56	2.43

PAN TROGL DYTES -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BPINDEX	CRINDEX	FERINDEX	HUMINDEX
BM(NH)	1951.9.27.6	493.45	109.00	91.00	78.00	25.00	25.00
BM(NH)	1948.5.7.2	569.70	104.00	90.00	83.00	22.00	23.00
BM(NH)	39.3366	0.00	116.00	95.00	84.00	27.00	23.00
BM(NH)	1956.5.27.1	508.95	110.00	97.00	79.00	26.00	25.00
BM(NH)	39.3367	426.25	109.00	93.00	80.00	24.00	22.00
BM(NH)	1948.10.25.2	477.50	107.00	102.00	82.00	24.00	24.00
BM(NH)	1976.437	2.42	5.45	2.35	52.20	52.28	0.00
POWELL COTTON	967	0.00	110.00	94.00	79.00	28.00	27.00
POWELL COTTON	800	0.00	107.00	91.00	78.00	24.00	23.00
POWELL COTTON	664	0.00	112.00	91.00	79.00	21.00	19.00
POWELL COTTON	655	0.00	110.00	89.00	81.00	22.00	20.00
POWELL COTTON	650	0.00	110.00	95.00	83.00	24.00	22.00
POWELL COTTON	504	0.00	110.00	93.00	82.00	26.00	23.00
POWELL COTTON	501	0.00	111.00	87.00	80.00	26.00	23.00
POWELL COTTON	493	0.00	113.00	87.00	81.00	27.00	24.00
POWELL COTTON	467	0.00	104.00	92.00	77.00	25.00	25.00
POWELL COTTON	450	0.00	109.00	92.00	80.00	24.00	24.00
	N	6	17	17	17	17	17
	MEAN	460.46	109.06	87.41	80.35	23.53	23.35
	STD. DEVIATION	56.60	3.33	22.73	1.97	5.85	1.93

PONGO PYG AEUS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRIINDEX	CRINDEX	FERIINDEX	HURINDEX
B4(NH)	302	502.80	144.00	104.00	82.00	24.00	21.00
B4(NH)	1084	475.75	0.00	95.00	0.00	0.00	21.00
B4(NH)	1093	448.15	143.00	96.00	83.00	25.00	20.00
B4(NH)	1950.6.10.1	509.15	0.00	0.00	88.00	25.00	0.00
B4(NH)	1973.1570	491.65	135.00	103.00	89.00	28.00	26.00
B4(NH)	31	501.65	142.00	100.00	84.00	23.00	20.00
B4(NH)	1944.10.25.1	486.75	140.00	105.00	83.00	24.00	22.00
B4(NH)	1080	494.85	141.00	103.00	87.00	26.00	23.00
B4(NH)	15 5.10.2.1	482.50	145.00	100.00	89.00	28.00	22.00
B4(NH)	1868.4.16.2	459.20	142.00	107.00	84.00	24.00	23.00
	N	10	8	9	9	9	9
	MEAN	475.03	141.50	101.44	85.44	25.22	22.00
	STD. DEVIATION	31.89	3.07	4.03	2.79	1.79	1.67

PONGO PYGMAEUS -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRIINDEX	CRINDEX	FERIINDEX	HURINDEX
B4(NH)	1950.4.10.2	0.00	141.00	103.00	84.00	24.00	22.00
B4(NH)	1948.7.6.1	395.65	143.00	102.00	84.00	23.00	19.00
B4(NH)	3P	0.00	143.00	103.00	83.00	21.00	18.00
CAM. DUCK.	51.0.5	372.45	138.00	100.00	83.00	24.00	21.00
	N	2	4	4	4	4	4
	MEAN	384.05	141.25	102.00	83.50	23.00	20.00
	STD. DEVIATION	16.40	2.36	1.41	0.58	1.41	1.83

HYLOBATES LLERI -- MALE AND FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMIINDEX	BRIINDEX	CRIINDEX	FERIINDEX	HUMINDEX
CAM. VET. A.A.	13	0.00	0.00	0.00	0.00	0.00	0.00
CAM. VET. A.A.	M1	0.00	0.00	0.00	0.00	0.00	0.00
CAM. VET. A.A.	M	0.00	0.00	0.00	0.00	0.00	0.00
CAM. VET. A.A.	M13	0.00	0.00	0.00	0.00	0.00	0.00
CAM. ZOO.	E71J0A	0.00	0.00	0.00	0.00	0.00	0.00
CAM. DUCK.	54.8.1	0.00	0.00	0.00	0.00	0.00	0.00
	N	3	6	6	6	6	6
	MEAN	278.96	134.33	114.50	86.00	16.00	13.17
	STD. DEVIATION	14.60	1.86	2.17	1.79	1.10	0.75

COLOBUS POLYKOMOS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMIINDEX	BRIINDEX	CRIINDEX	FERIINDEX	HUMINDEX
BM(NH)	1930.5.1.13	369.75	83.00	97.00	88.00	21.00	24.00
BM(NH)	1180A	395.90	77.00	100.00	86.00	17.00	21.00
BM(NH)	1930.12.15.1	436.40	78.00	99.00	89.00	18.00	22.00
POWELL COTTON	98	0.00	82.00	100.00	91.00	21.00	23.00
	N	3	4	4	4	4	4
	MEAN	400.68	80.00	99.00	88.50	19.25	22.50
	STD. DEVIATION	33.58	2.94	1.41	2.08	2.06	1.95

COLOBUS POLYKOMOS -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMIINDEX	BRIINDEX	CRIINDEX	FERIINDEX	HUMINDEX
BM(NH)	1939.4.21.2	385.05	82.00	97.00	91.00	19.00	20.00
BM(NH)	72.158	411.65	81.00	101.00	93.00	20.00	22.00
	N	2	2	2	2	2	2
	MEAN	398.35	81.50	99.00	92.00	19.50	21.00
	STD. DEVIATION	19.81	0.71	2.83	1.41	0.71	1.41

COLOURS [illegible] -- MALE

COLLECTION	SPECIMEN NO.	STLE 4G	IMIINDEX	BRINDEX	CRINDEX	FERINDEX	HUMINDEX
BM(NH)	1930.8.1.2	395.50	89.00	95.00	87.00	21.00	24.00
BM(NH)	1930.8.1.1	385.10	86.00	103.00	87.00	20.00	23.00
BM(H)	1940.106	341.20	90.00	100.00	86.00	21.00	24.00
BM(NH)	1965.7.25.1	360.50	86.00	98.00	85.00	18.00	21.00
BM(NH)	1916.6.5.1	374.25	82.00	99.00	87.00	19.00	21.00
BM(NH)	1931.8.9.46	384.20	90.00	94.00	85.00	21.00	22.00
BM(NH)	72.153	354.70	0.00	0.00	0.00	20.00	22.00
	N	7	6	6	6	7	7
	MEAN	369.35	87.17	95.17	86.17	20.00	22.43
	STD. DEVIATION	17.51	3.13	3.31	0.98	1.15	1.27

COLOURS BALLOS -- FEMALE

COLLECTION	SPECIMEN NO.	STLE 4G	IMIINDEX	BRINDEX	CRINDEX	FERINDEX	HUMINDEX
CAM. DUCK.	40.109	384.75	89.00	100.00	87.00	19.00	23.00
CAM. DUCK.	778.13	410.45	87.00	96.00	84.00	19.00	22.00
CAM. DUCK.	1933.3.1.6	331.15	84.00	98.00	89.00	18.00	20.00
CAM. DUCK.	72.152	348.20	0.00	0.00	0.00	19.00	22.00
POWELL COTTON	215	0.00	90.00	101.00	87.00	20.00	23.00
	N	4	4	4	4	5	5
	MEAN	368.64	87.50	98.75	86.75	19.00	22.00
	STD. DEVIATION	35.73	2.65	2.22	2.06	0.71	1.22

COLOR'S OF LETA -- MALE

COLLECTI	SPECIMEN NO.	STLENG	IMIINDEX	BRIINDEX	CRIINDEX	FERIINDEX	MORIINDEX
B4(NH)	72.144	362.65	81.00	97.00	90.00	20.00	21.00
B4(NH)	72.141	357.35	0.00	0.00	0.00	20.00	23.00
B4(NH)	72.139	402.35	0.00	0.00	0.00	21.00	24.00
B4(NH)	72.134	392.30	0.00	0.00	0.00	20.00	21.00
B4(NH)	72.151	377.75	0.00	0.00	0.00	19.00	21.00
B4(NH)	72.152	392.45	0.00	0.00	0.00	19.00	22.00
	N	6	1	1	1	6	6
	MEAN	377.43	81.00	97.00	90.00	19.83	22.00
	STD. DEVIATION	24.15	0.00	0.00	0.00	4.45	1.26

COLOR'S OF LEZA -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMIINDEX	BRIINDEX	CRIINDEX	FERIINDEX	MORIINDEX
B4(NH)	72.148	364.40	83.00	95.00	89.00	20.00	20.00
B4(NH)	72.150	320.35	0.00	0.00	0.00	20.00	21.00
B4(NH)	72.138	407.65	0.00	0.00	0.00	21.00	23.00
B4(NH)	72.140	418.05	0.00	0.00	0.00	20.00	22.00
B4(NH)	72.153	402.65	0.00	0.00	0.00	19.00	20.00
	N	5	1	1	1	5	5
	MEAN	382.62	83.00	95.00	89.00	20.00	21.20
	STD. DEVIATION	40.29	0.00	0.00	0.00	0.71	1.30

PRESBYTIS [illegible] -- MALE

COLLECTION	SPECIMEN NO.	STLE.G	IMTINDEX	MPINDEX	CRI.DEX	FERINDEX	HJRINDEX
BM(NH)	71.733	346.15	83.00	95.00	89.00	18.00	20.00
BM(NH)	71.739	325.50	86.00	100.00	87.00	20.00	20.00
BM(NH)	71.734	347.70	83.00	95.00	84.00	20.00	21.00
BM(NH)	71.722	341.65	81.00	96.00	85.00	18.00	21.00
BM(NH)	71.718	0.00	84.00	101.00	86.00	20.00	22.00
BM(NH)	71.728	333.15	83.00	100.00	83.00	19.00	23.00
BM(NH)	71.732	348.55	84.00	95.00	85.00	19.00	21.00
BM(NH)	71.735	335.55	83.00	98.00	87.00	19.00	21.00
BM(NH)	71.729	354.50	83.00	96.00	87.00	20.00	23.00
	N	8	9	9	9	9	9
	MEAN	342.22	83.33	97.67	85.89	19.22	21.33
	STD. DEVIATION	9.08	1.32	2.29	1.83	0.83	1.12

PRESBYTIS [illegible] -- FEMALE

COLLECTION	SPECIMEN NO.	STLE.G	IMTINDEX	MPINDEX	CRI.DEX	FERINDEX	HJRINDEX
BM(NH)	71.711	0.00	85.00	97.00	87.00	19.00	19.00
BM(NH)	71.707	0.00	87.00	98.00	86.00	18.00	19.00
BM(NH)	71.724	343.10	85.00	97.00	88.00	20.00	21.00
BM(NH)	71.708	0.00	87.00	99.00	86.00	20.00	22.00
BM(NH)	71.710	351.65	84.00	98.00	84.00	19.00	22.00
BM(NH)	71.720	362.75	86.00	101.00	87.00	21.00	23.00
BM(NH)	71.719	354.80	86.00	99.00	86.00	19.00	20.00
BM(NH)	71.751	347.10	84.00	100.00	88.00	20.00	22.00
BM(NH)	71.721	365.00	83.00	98.00	84.00	19.00	22.00
BM(NH)	71.737	330.20	87.00	97.00	88.00	20.00	20.00
BM(NH)	71.703	325.35	86.00	97.00	85.00	19.00	22.00
BM(NH)	71.736	341.60	83.00	98.00	87.00	21.00	23.00
BM(NH)	71.705	346.15	83.00	99.00	85.00	19.00	21.00
	N	10	13	13	13	13	13
	MEAN	347.07	85.08	98.23	86.38	19.54	21.23
	STD. DEVIATION	13.20	1.55	1.24	1.50	0.88	1.36

CERCOCEBUS TORQUATUS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1948.45.1	387.55	86.00	103.00	87.00	20.00	23.00
BM(NH)	1948.7.7.3	346.90	86.00	105.00	89.00	21.00	23.00
	N	2	2	2	2	2	2
	MEAN	364.73	86.00	104.00	88.00	20.50	23.00
	STD. DEVIATION	25.21	0.00	1.41	1.41	0.71	0.00

CERCOCEBUS TORQUATUS -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1959.2.8.2	297.70	85.00	102.00	88.00	21.00	22.00
BM(NH)	193 .12.6.1	326.85	86.00	103.00	89.00	19.00	21.00
BM(NH)	1938.7.7.4	320.90	85.00	103.00	91.00	22.00	23.00
BM(NH)	1953.7.7.5	321.30	87.00	102.00	89.00	21.00	22.00
	N	4	4	4	4	4	4
	MEAN	316.69	85.75	102.50	89.25	20.75	22.00
	STD. DEVIATION	12.95	0.96	0.58	1.26	1.26	0.82

CERCOCEBUS ALBIGENA -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1930.8.1.25	341.25	82.00	95.00	88.00	17.00	20.00
BM(NH)	72.21	345.50	0.00	0.00	0.00	19.00	22.00
POWELL COTTON	693	0.00	82.00	102.00	91.00	18.00	21.00
POWELL COTTON	339	0.00	80.00	97.00	99.98	18.00	19.00
POWELL COTTON	798	0.00	81.00	101.00	89.00	19.00	23.00
POWELL COTTON	668	0.00	80.00	102.00	93.00	19.00	21.00
POWELL COTTON	371	0.00	83.00	98.00	90.00	19.00	22.00
POWELL COTTON	852	0.00	81.00	102.00	91.00	18.00	21.00
POWELL COTTON	749	0.00	82.00	94.00	90.00	19.00	21.00
	N	2	8	8	8	9	9
	MEAN	343.38	81.38	98.88	91.63	18.44	21.11
	STD. DEVIATION	3.01	1.06	3.31	4.07	0.73	1.17

CEPHOPHUS [illegible] -- FEMALE

COLLECTION	SPECIMEN NO.	STLE IG	IMINDEX	BMINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	72.22	313.45	0.00	0.00	0.00	18.00	21.00
POWELL COTTON	355	0.00	81.00	97.00	90.00	19.00	21.00
POWELL COTTON	997	0.00	83.00	98.00	90.00	18.00	20.00
POWELL COTTON	157	0.00	82.00	105.00	93.00	18.00	20.00
POWELL COTTON	736	0.00	82.00	95.00	90.00	18.00	20.00
POWELL COTTON	561	0.00	81.00	100.00	92.00	18.00	20.00
POWELL COTTON	721	0.00	82.00	100.00	93.00	19.00	21.00
POWELL COTTON	997	0.00	83.00	100.00	86.00	20.00	24.00
	8	1	7	7	7	8	8
	MEAN	313.45	82.00	99.43	90.57	18.50	20.88
	STD. DEVIATION	0.00	0.82	1.99	2.44	0.76	1.36

CEPHOPHUS [illegible] ITIS -- MALE

COLLECTIO	SPECIMEN NO.	STLE IG	IMINDEX	B INDEX	CRI.DEX	FERINDEX	HURINDEX
BM(NH)	72.76	371.10	0.00	0.00	0.00	21.00	23.00
BM(NH)	72.68	333.50	0.00	0.00	0.00	21.00	23.00
BM(NH)	72.82	353.35	82.00	97.00	94.00	20.00	23.00
BM(NH)	72.88	328.65	84.00	96.00	97.00	20.00	22.00
BM(NH)	72.72	331.45	0.00	0.00	0.00	20.00	20.00
BM(NH)	72.60	374.00	0.00	0.00	0.00	21.00	23.00
BM(NH)	72.90	384.30	81.00	100.00	93.00	20.00	23.00
BM(NH)	72.65	362.15	85.00	96.00	94.00	20.00	24.00
BM(NH)	72.59	385.25	0.00	0.00	93.00	21.00	0.00
BM(NH)	72.53	315.05	0.00	0.00	0.00	21.00	22.00
BM(NH)	72.52	353.85	0.00	0.00	0.00	19.00	21.00
	9	11	4	4	5	11	10
	MEAN	354.65	83.00	97.25	94.20	20.36	20.40
	STD. DEVIATIO	25.60	1.93	1.89	1.64	0.67	6.22

CERCOPITHECUS AETHIOPS -- FEMALE

COLLECTION	SPECIMEN NO.	STLE IG	IMINDEX	BRIINDEX	CRIINDEX	FERINDEX	MURIINDEX
BM(NH)	72.79	331.45	84.00	95.00	95.00	20.00	21.00
BM(NH)	72.85	319.80	83.00	95.00	93.00	20.00	23.00
BM(NH)	72.78	283.95	0.00	0.00	0.00	22.00	23.00
BM(NH)	72.83	322.25	83.00	91.00	92.00	20.00	22.00
BM(NH)	72.87	321.30	86.00	97.00	96.00	19.00	22.00
BM(NH)	72.77	301.50	0.00	0.00	0.00	20.00	22.00
BM(NH)	72.81	301.05	84.00	95.00	95.00	21.00	23.00
BM(NH)	72.83	352.25	0.00	0.00	0.00	21.00	23.00
BM(NH)	72.86	325.60	86.00	95.00	95.00	21.00	22.00
BM(NH)	72.55	305.25	83.00	95.00	95.00	18.00	20.00
BM(NH)	72.82	281.60	84.00	96.00	96.00	21.00	23.00
BM(NH)	72.54	313.70	0.00	0.00	0.00	20.00	20.00
	N	12	8	8	8	12	12
	MEAN	313.31	84.13	94.88	93.38	20.25	22.00
	STD. DEVIATION	19.95	1.25	1.73	1.51	1.06	1.13

CERCOPITHECUS AETHIOPS -- FEMALE

COLLECTION	SPECIMEN NO.	STLE IG	IMINDEX	BRIINDEX	CRIINDEX	FERINDEX	MURIINDEX
BM(NH)	72.33	264.00	0.00	0.00	0.00	19.00	23.00
BM(NH)	72.32	249.80	0.00	0.00	0.00	20.00	22.00
BM(NH)	1930.1.1.15	291.75	89.00	98.00	94.00	20.00	24.00
BM(NH)	72.30	301.30	0.00	0.00	0.00	22.00	24.00
BM(NH)	72.27	289.20	0.00	0.00	0.00	22.00	25.00
BM(NH)	72.50	271.05	0.00	0.00	0.00	22.00	24.00
	N	6	1	1	1	6	6
	MEAN	277.85	89.00	98.00	94.00	20.83	23.67
	STD. DEVIATION	19.48	0.00	0.00	0.00	1.33	1.03

CERCOPITHECUS AETHIOPS -- MALE

COLLECTIO.	SPECIMEN NO.	STLE G	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HUMINDEX
B4(NH)	72.33	0.00	0.00	0.00	0.00	20.00	21.00
B4(NH)	72.25	0.00	0.00	0.00	0.00	21.00	23.00
B4(NH)	72.29	0.00	0.00	0.00	0.00	19.00	22.00
B4(NH)	72.31	0.00	0.00	0.00	0.00	18.00	22.00
	N	3	0	0	0	4	4
	MEAN	303.07	0.00	0.00	0.00	19.50	22.00
	STD. DEVIATION	12.93	0.00	0.00	0.00	1.29	0.85

CERCOPITHECUS NEGLECTUS -- MALE

COLLECTIO.	SPECIMEN NO.	STLE.G	IMI.DEX	BRINDEX	CRI DEX	FERI.DEX	HURINDEX
B4(NH)	1972.47	353.20	83.00	94.00	95.00	20.00	23.00
B4(NH)	1972.50	376.05	84.00	93.00	94.00	22.00	25.00
POWELL COTT.	372	0.00	87.00	97.00	97.00	21.00	24.00
	N	2	3	3	3	3	3
	MEAN	303.13	84.67	94.67	95.33	21.00	24.00
	STD. DEVIATION	15.28	2.08	2.08	1.53	1.00	1.00

CERCOPITHECUS NEGLECTUS -- FEMALE

COLLECTIO	SPECIMEN NO.	STLENG	IMINDEX	BRI.DEX	CRI.DEX	FERI.DEX	HURINDEX
B4(NH)	1972.49	284.85	87.00	90.00	92.00	21.00	23.00
B4(NH)	1972.48	304.10	84.00	91.00	93.00	21.00	23.00
B4(NH)	1972.45	303.20	0.00	0.00	0.00	23 00	25.00
	N	3	2	2	2	3	3
	MEA.	299.05	85.50	90.50	92.50	21.67	23.67
	STD. DEVIATIO.	7.98	2.12	0.71	0.71	1.15	1.15

CERCOPITHECUS [illegible] -- MALE

COLLECTIC	SPECIMEN NO.	STLENG	IMINDEX	BRIINDEX	CRINDEX	FERINDEX	MURINDEX
BM(NH)	1946.469	312.15	0.00	0.00	96.00	20.00	0.00
BM(NH)	1948.481	321.75	82.00	98.00	96.00	20.00	23.00
BM(NH)	1948.477	353.55	86.00	102.00	97.00	20.00	25.00
BM(NH)	1946.480	306.20	85.00	96.00	92.00	22.00	24.00
BM(NH)	1948.475	316.95	86.00	103.00	96.00	21.00	23.00
BM(NH)	1948.7.7.8	321.00	83.00	99.00	96.00	20.00	22.00
BM(NH)	1948.7.7.9	331.65	83.00	89.00	97.00	20.00	22.00
	8	7	6	6	7	7	6
	MEAN	323.18	84.17	97.83	95.71	21.43	23.17
	STD. DEVIATION	15.57	1.72	5.04	1.70	0.79	1.17

CERCOPITHECUS TALAPOI -- MALE

COLLECTIC	SPECIMEN NO.	STLENG	IMINDEX	BRIINDEX	CRINDEX	FERINDEX	MURINDEX
BM(NH)	1977.874	200.75	85.00	98.00	98.00	21.00	22.00
BM(NH)	1977.880	184.85	85.00	96.00	97.00	20.00	23.00
BM(NH)	1977.884	210.10	86.00	103.00	99.99	21.00	21.00
	3	3	3	3	3	3	3
	MEAN	198.57	85.33	99.00	98.33	20.67	22.00
	STD. DEVIATION	12.77	0.58	3.61	1.53	0.58	1.00

CERCOPITHECUS TALAPOI -- FEMALE

COLLECTIO	SPECIMEN NO.	STLENG	IMINDEX	BRIINDEX	CRINDEX	FERINDEX	MURINDEX
BM(NH)	1977.870	183.75	87.00	101.00	97.00	20.00	21.00
BM(NH)	1977.881	189.45	86.00	99.00	96.00	21.00	21.00
BM(NH)	1977.882	194.85	85.00	99.00	98.00	20.00	22.00
BM(NH)	1977.867	0.00	86.00	103.00	99.99	21.00	23.00
BM(NH)	1977.873	184.55	87.00	99.00	97.00	21.00	22.00
	4	4	5	5	5	5	5
	MEAN	188.15	86.20	100.20	97.60	20.60	21.80
	STD. DEVIATION	13.72	0.84	1.79	1.52	0.55	0.84

MACACA FASCICULARIS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1957.12.11.5	268.60	95.00	102.00	91.00	23.00	23.00

MACACA FASCICULARIS -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1894.6.12.13	265.70	97.00	96.00	90.00	22.00	20.00
BM(NH)	1930.12.24.1	275.75	95.00	99.00	96.00	22.00	22.00
	N	2	2	2	2	2	2
	MEAN	271.23	96.00	97.50	93.00	22.00	21.00
	STD. DEVIATION	7.81	1.41	2.12	4.24	0.00	1.41

MACACA [illegible] -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM( )	5[illegible].15.2	256.15	96.00	103.00	91.00	24.00	25.00

MACACA [illegible] -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	333	298.60	90.00	101.00	93.00	22.00	24.00

MACACA DE ELTRIA -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1933.11.9.1	273.75	98.00	104.00	90.00	22.00	25.00

MACACA SILVANUS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1858.4.5.1	347.60	91.00	105.00	88.00	23.00	26.00

MACACA SILVANUS -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1854.3.20.1	365.15	90.00	100.00	88.00	24.00	25.00

CYNOPITHECUS NIGER -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1946.5.18.1	261.49	94.00	102.00	90.00	21.00	23.00

PAPIO HAMADRYAS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1935.2.14.1	442.45	101.00	106.00	85.00	24.00	25.00
BM(NH)	1948.4.3.2	363.40	100.00	107.00	86.00	23.00	24.00
BM(NH)	1962.6.26.1	433.70	103.00	109.00	83.00	21.00	21.00
	N	3	3	3	3	3	3
	MEAN	413.18	101.33	107.33	84.67	22.67	23.33
	STD. DEVIATION	43.34	1.53	1.53	1.53	1.53	2.08

PAPIO HAMADRYAS -- FEMALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1901.6.9.23	355.95	103.00	106.00	86.00	21.00	21.00
BM(NH)	1962.12.14.6	348.25	100.00	103.00	85.00	23.00	23.00
BM(NH)	1962.6.26.2	380.95	102.00	106.00	83.00	21.00	22.00
	N	3	3	3	3	3	3
	MEAN	361.72	101.67	105.00	84.67	21.67	22.00
	STD. DEVIATION	17.10	1.53	1.73	1.53	1.15	1.00

PAPIO URSINUS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1975.1290	423.80	96.00	106.00	86.00	23.00	26.00

PAPIO CYNOCEPHALUS -- MALE

COLLECTION	SPECIMEN NO.	STLENG	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1962.7.6.13	378.45	99.00	104.00	85.00	21.00	22.00
BM(NH)	1972.129	418.60	99.00	111.00	87.00	19.00	21.00
	N	2	2	2	2	2	2
	MEAN	398.53	99.00	107.50	86.00	20.00	21.50
	STD. DEVIATION	28.39	0.00	4.95	1.41	1.41	0.71

ALOUATTA [illegible] -- FEMALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1934.7.6.1.2	0.00	97.00	92.00	84.00	19.00	20.00

ALOUATTA PALLIATA -- MALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1952.857	0.00	98.00	88.00	88.00	21.00	21.00

ALOUATTA SENICULUS -- FEMALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1931.10.16.1	285.05	98.00	88.00	83.00	21.00	19.00

ATELES PANISCUS -- SEX UNKNOWN

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	93.7.22.19	321.00	105.00	97.00	91.00	20.00	16.00

BRACHYTELES ARACHNOIDES -- SEX UNKNOWN

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1845.6.21.4	302.80	107.00	96.00	85.00	19.00	17.00

CEBUS [illegible] -- FEMALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	3.9.1.5	0.00	81.00	94.00	90.00	18.00	21.00

CEBUS APELLA -- MALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	3.9.1.4	0.00	84.00	96.00	90.00	20.00	25.00

CEBUS APELLA -- FEMALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	1966.10.20.2	311.30	85.00	91.00	89.00	19.00	22.00

LAGOTHRIX LAGOTHRICHA -- FEMALE

COLLECTION	SPECIMEN NO.	STATURE	IMINDEX	BRINDEX	CRINDEX	FERINDEX	HURINDEX
BM(NH)	72.1926	259.75	97.00	85.00	87.00	24.00	22.00

Appendix II. Higher Primate Body Weights

Key to the Abbreviations used in Appendix II

♀ X Weight	Female mean body weight in grams
N	Sample size
C	captive animals
W	wild animals
♂ X Weight	Male mean body weight in grams

Arboreal Quadrupedalism -- Small Size -- Clawed		♀ X̄ Weight	N	C/W	♂ X̄ Weight	N	C/W
Callimico	C. goeldii	470	?	C	472	?	C
Callithrix	C. argentatus	419	?	C	413	2	C
	C. jacchus	275	24	C	289	20	C
Cebuella	C. pygmaea	136	6	C	158	4	C
Saguinus	S. fuscicattis	450	1	C	450	1	C
	S. geoffroyi	510	2	W	500	3	W
	S. midas	529	4	W	595	4	W
	S. nigricollis	350	1	C			
	S. oedipus	512	2	C	450	1	C
Arboreal Quadrupedalism -- Medium Size							
Aotus	A. trivirgatus	998	6	C	972	5	C
Cacajao	C. rubicundus				3750	2	C
Callicebus	C. moloch	1056	?	C	1100	?	C
Cebus	C. apella	1804	7	C/W	2862	3	C
	C. capucinus	2700	4	C	3821	6	C
	C. albifrons				2400	1	C
	C. nigrivitattus				2996	2	C
Chiropotes	C. chiroptes				2950	1	W
Pithecia	P. pithecia	1516	4	W	1578	6	W
Saimiri	S. oerstedi	603	3	C	907	3	C
	S. sciureus	775	8	W	1052	2	W

Arboreal Quadrupedalism -- Large Size -- Branch Sitting and Walking		♀ $\bar{X}$ Weight	N	C/W	♂ $\bar{X}$ Weight	N	C/W
Cercocebus	C. albigena	6203	15	W	9010	16	W
	C. galeritus	5473	3	W	10183	3	W
	C. torquatus	7420	4	C			
Cercopithecus	C. aethiops	3644	4	W	4750	4	W
	C. albogularis	4533	1	C	6349	1	C
	C. ascanius	2926	43	W	4284	43	W
	C. cephus	2882	10	W	4087	8	W
	C. lhoesti	4700	1	W	8500	1	W
	C. mitis	4395	7	W	7599	11	W
	C. mona	2500	1	W	4458	4	C/W
	C. neglectus	3960	4	W	7000	4	W
	C. nictitans	4216	9	W	6600	16	W
	C. pogonias	3025	6	W	4500	4	W
	C. pygerythrus	3021	3	W	5378	5	W
	C. diana	5527	3	C	6200	1	C
	C. talapoin	1036	22	C/W	1424	17	C/W
Arboreal Quadrupedalism -- Old World Semibrachiation -- Large Size							
Colobus	C. badius	6512	7	W	9220	2	W
	C. guereza	7941	7	W	10017	4	W
	C. polykomos	8369	11	C/W	11250	2	C/W
	C. verus	3600	5	W	3800	7	W
Nasalis	N. larvatus	9873	15	W	20334	10	W
Presbytis	P. obscura	6871	11	W	7593	7	W

Arboreal Quadrupedalism -- Large Size -- New World Semibrachiation		♀ $\bar{X}$ Weight	N	C/W	♂ $\bar{X}$ Weight	N	C/W
Alouatta	A. caraya	5700	2	C	7616	79	W
	A. seniculus	5720	4	W	7392	4	W
	A. villosa	6000	4	C	7257	7	W
Ateles	A. fusciceps	9163	10	C	8890	6	C
	A. geoffroyi	8620	18	C	7764	8	C
	A. paniscus				6589	3	C
Lagothrix	L. lagothricha	6362	8	C	6133	3	C
Part Terrestrial Quadrupedalism and Part Arboreal Quadrupedalism							
Cynopithecus	C. niger	6214	14	C	7364	4	C
Macaca	M. assamensis	6115	4	W	7833	3	W
	M. fuascicularis	3489	10	C/W	4728	14	C/W
	M. fuscata	9141	81	W	11767	49	W
	M. mulatta	5999	18	C/W	8676	5	C/W
	M. nemestrina	6335	18	C/W	9955	10	C/W
	M. radiata	3685	8	C	6599	8	C
	M. sylvanus	9109	3	C	15100	1	C
	M. sinica	3400	1	C	6500	1	C
Mandrillus	M. leucophaeus	8450	2	C	21400	1	C
	M. sphinx	10100	1	W	19500	1	C
Terrestrial Quadrupedalism -- Ground Standing and Walking							
Erythrocebus	E. patas	6317	3	C	12600	1	W
Papio	P. anubis	12200	237	W	21100	177	W
	P. cynocephalus	10200	1	C	19350	?	C
	P. hamadryas	10300	4	C	21500	6	C
	P. papio	16166	5	C	19025	4	C
	P. ursinus	16818	?	W	20454	?	W

Brachiation		♀ $\bar{X}$ Weight	N	C/W	♂ $\bar{X}$ Weight	N	C/W
Hylobates	H. agilis	5440	6	W	5984	?	W
	H. concolor	5800	11	W	5600	10	W
	H. hoolock	6500	2	W	6 00	5	W
	H. klossii	5900	4	W	5700	2	W
	H. lar	5228	45	W	5655	56	W
	H. moloch	5667	6	W	5967	12	W
	H. mulleri				5700*	?	W
Symphalangus	S. syndactylus	10600	9	W	10850	10	W
Bipedalism							
Homo	H. sapiens - caucasian	58620	1126	-	73490	956	-
	H. sapiens - negro	56700	147	-	74900	62	-
Knuckle Walking (Pan and Gorilla)							
Gorilla	G. gorilla	81679	5	C/W	139680	32	W
Pan	P. paniscus	37750	2	C	45500	1	C
	P. troglodytes	41083	6	C/W	49056	6	C/W
Pongo	P. pygmaeus	37420	10	C	72750	9	C

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